ISSN 2789-2786

CAPITULUM

THE INTERNATIONAL COMPOSITAE ALLIANCE NEWSLETTER

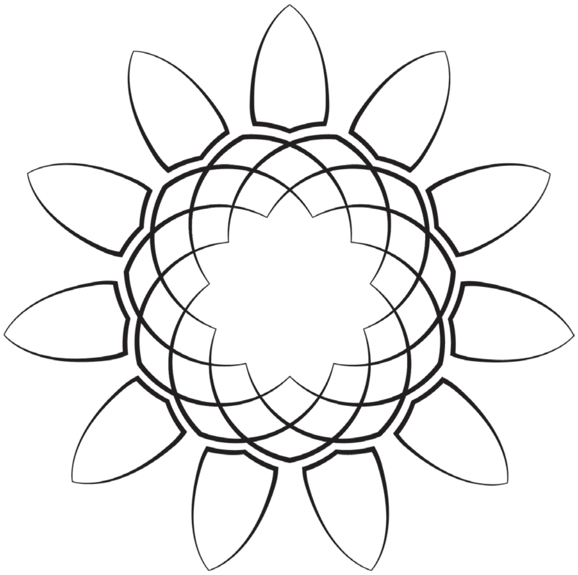
TICA

THE INTERNATIONAL COMPOSITAE ALLIANCE

VOLUME 3(2) - JANUARY 2025

CAPITULUM

THE INTERNATIONAL COMPOSITAE ALLIANCE NEWSLETTER



CAPITULUM
For the community, by the community.

TICA
THE INTERNATIONAL COMPOSITAE ALLIANCE

CAPITULUM

THE INTERNATIONAL COMPOSITAE ALLIANCE NEWSLETTER

CAPITULUM

CAPITULUM is the Newsletter of The International Compositae Alliance
and is meant to be a venue for all things Compositae and welcomes all kinds of diversity
in both its contributions and contributors. ISSN 2789-2786.

EDITORS-in-CHIEF

Jennifer R. Mandel
University of Memphis, Tennessee, USA
jmandel@memphis.edu

Mauricio Bonifacino
Universidad de la República, Montevideo, URUGUAY
mbonifa@gmail.com

EDITORIAL BOARD

Ilse Breitwieser
Allan Herbarium – Landcare Research, NEW ZEALAND
breitwieseri@landcareresearch.co.nz

Isaac Lichter-Mark
California Academy of the Sciences, San Francisco, California, U.S.A
ilichtermarck@gmail.com

Benoit Loeuille
Royal Botanic Gardens, Kew, UK
b.loeuille@kew.org

Abigail Moore
University of Oklahoma, USA
abigail.j.moore@ou.edu

Erika R. Moore-Pollard
University of Memphis, Tennessee, USA
ermoore3@memphis.edu

Luis Palazzesi
Museo Argentino de Ciencias Naturales, ARGENTINA
lpalazzesi@gmail.com

Lizzie Roeble
Naturalis Biodiversity Center, THE NETHERLANDS
lizzie.roeble@naturalis.nl

Gisela Sancho
Museo de la Plata, ARGENTINA
sancho@fcnym.unlp.edu.ar

Alexander N. Schmidt-Lebuhn
CSIRO, Centre for Australian National Biodiversity Research, AUSTRALIA
Alexander.S-L@csiro.au

Ed Schilling
University of Tennessee, USA
eschilling@utk.edu

Alfonso Susanna
Botanic Institute of Barcelona, SPAIN
asusanna@ibb.csic.es

Yannick Woudstra
Stockholm University, SWEDEN
yannickwoudstra@outlook.com

SUBMISSIONS

Manuscripts or photos intended for publication in CAPITULUM
are to be submitted at www.compositae.org

Copyright © 2025 TICA | The International Compositae Alliance

CAPITULUM
THE INTERNATIONAL COMPOSITAE ALLIANCE NEWSLETTER
VOLUME 3(2) -JANUARY 2025

DOI: http://dx.doi.org/10.53875/capitulum.03.2

CONTENTS

HEAD TOPICS
Styles of Asteraceae: A synopsis of their morphological and functional diversity | 1
Claudia Erbar & Peter Leins

BREVIA
Taraxacum F.H.Wigg. (Cichorieae) in Australia: The story of systematic research on the island continent in the last four decades | 39
Robert F. Parsons

THE CABINET
Charles Jeffrey: polyglot, synantherologist and cucurbitologist | 46
D.J. Nicholas Hind

STYLE | 59

TICA TIMES | 62

GUIDELINES FOR AUTHORS | 64

Cover photo: *Gymnocoronis spilanthoides* DC., featuring a discoid capitulum in which all the visually appealing structures are the style branches. Artigas, Uruguay.
Photo by Mauricio Bonifacino

Styles of Asteraceae:

A synopsis of their morphological and functional diversity

Claudia Erbar[1] & Peter Leins[1]

[1] Centre for Organismal Studies (COS), Faculty of Biosciences, Heidelberg University, Germany; *claudia.erbar@alumni.uni-heidelberg.de, erle@urz.uni-heidelberg.de*

Author for correspondence: Claudia Erbar, *claudia.erbar@alumni.uni-heidelberg.de*

DOI: http://dx.doi.org/10.53875/capitulum.03.2.01

ABSTRACT

The style of an individual flower of the Asteraceae (or Compositae) is one of the most important floral organs in two respects. 1. It is important for the systematics of the family: its characters have significantly contributed to its past and present classification. 2. The styles in their different forms are essential components in the mechanisms of secondary pollen presentation. The latter ensures an optimization of pollination by pollen portioning, a widespread phenomenon in angiosperms. After a detailed study of style morphology (by SEM and sectioning) of more than 580 species of 346 genera covering all (presently accepted) 44 tribes of the Asteraceae, a total of 49 style types are established. Bringing together both morphology and function, the style types represent eight possibilities of secondary pollen presentation, which can be subsumed into four main functional categories: deposition, brushing, pump, and pump and brushing combined. From style characters and the position of the style tip within the anther tube shortly before anthesis, it is now in most cases easy to predict the mechanism of secondary pollen presentation. Pollen protection and pollen portioning are the two advantages achieved by secondary pollen presentation. Pollen portioning, the economical use of pollen grains, is one of the most important factors in the context of optimization of pollination. Particularly the pump mechanism seems to be an optimised mechanism in terms of pollen protection and refined pollen portioning (small pollen portions exuding from the five slits between the connective appendages (when looking from above, the "five-pointed star" is observable).

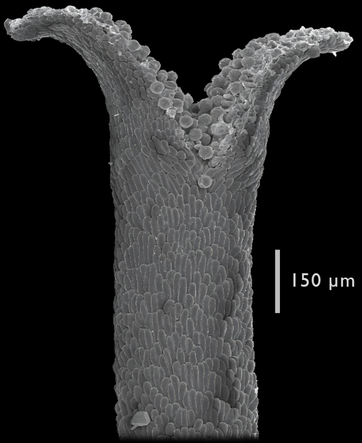
Keywords: Compositae, secondary pollen presentation

INTRODUCTION

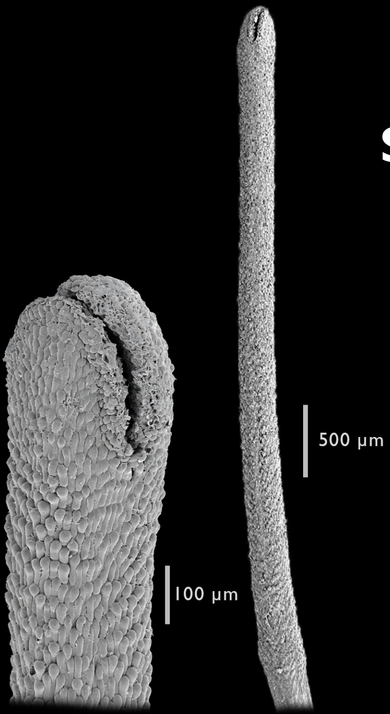
Organismal evolution is dominated by both chance events (e.g., mutation, recombination, migration, and isolation) as well as the principle of economy (optimization) through natural selection. For many years, this principle (giving rise to competition) was the focal point of interest in all our flower ecological and phylogenetic studies. We were particularly fascinated by the optimization of pollination. In this context, portioning of pollen is a widespread phenomenon. Pollen portioning is often achieved by successive opening of the anthers within a flower or by various mechanisms of secondary pollen presentation. The size of the pollen portion is connected with numerous different parameters within a highly complex, multifactorial network of correlations (see, e.g., Leins & Erbar, 2010). The most species-rich plant family, the Asteraceae, is characterized by particularly small pollen portions, which without exception are provided by secondary pollen presentation – most probably one of the key

The minimalist simplicity of the basal grade

The roughness of the style surface or the presence of distinct bulges is associated with mechanisms of secondary pollen presentation in early-diverging lineages. These mechanisms include simple brushing after deposition or a pump-like action, where apical thickening of the style branches blocks the lower opening of the anther tube, preventing pollen grains from falling out downwards.

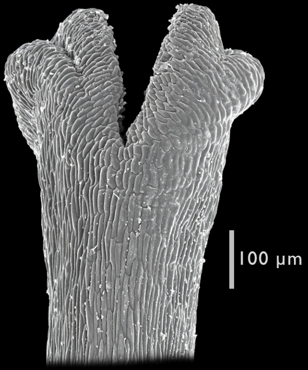


Arnaldoa macbrideana
BARNADESIEAE

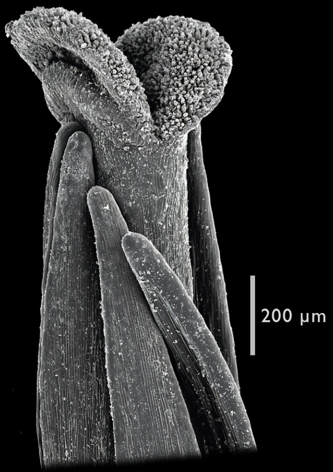


Schlechtendalia luzulifolia
BARNADESIEAE

Stifftia chrysantha
STIFFTIEAE

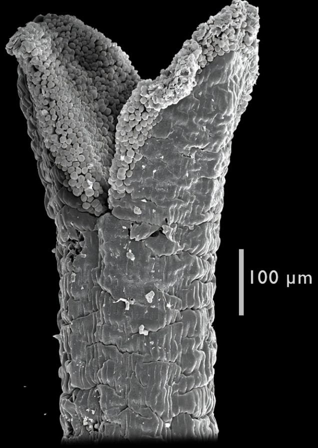


Barnadesia spinosa
BARNADESIEAE



Barnadesia arborea
BARNADESIEAE

Fulcaldea laurifolia
BARNADESIEAE



Famatinanthus decussatus
FAMATINANTHEAE

factors for the great evolutionary success of this family in terms of biodiversity (species richness) and distribution in different habitats nearly all over the world. The styles of the individual flowers play an important role within the different mechanisms of secondary pollen presentation.

Asteraceae show a great variety of styles, despite their very uniform flower structure. This diversity has fascinated synantherologists since the beginning of systematic studies of the family. Thus, style characteristics were an important feature for early classifications (into tribes) of this plant group. Most of the early studies on Compositae were illustrated by plates with details of inflorescences, floral parts, and in particular, styles. Starting with the small drawings of Tournefort (1700), Vaillant (1721), and Berkhey (1760), the illustrations became more informative when they were used for tribe characterisation by Cassini (e.g., 1826), Lessing (1832), Bentham (1873), and Hoffmann (1894). Of particular note are the six tables with excellent style drawings by Hildebrand (1870) that are often overlooked. Over time, further characteristics from different scientific disciplines (e.g., embryology, palynology, phytochemistry, and since the 1990s, molecular data) changed the taxonomic picture of the family, but style characteristics (still demonstrated by realistic illustrations) continued to play a role (e.g., Heywood et al., 1977; Bremer, 1994; Funk et al., 2009a).

We pursued two main objectives with our comprehensive study (Erbar & Leins, 2021). In a first step, we studied many styles throughout the whole family, reviving style morphology and anatomy. We considered, however, not only arrangement of the style trichomes, but also their shape and structure, the shape of the style branches and shaft as well as the location of the stigmatic tissue. We have done this with the understanding that the occurrence and position of style trichomes can be linked with the mode of secondary pollen presentation. The mechanism can often be inferred from the style characters (particularly in the pure brushing or pure pump mechanism). In a second step, we demonstrated modes of secondary pollen presentation in each of the 44 presently accepted tribes and 49 style types, the latter resulting from our comparative study. The possibilities of secondary pollen presentation found in Asteraceae can be categorized into eight mechanisms.

In this review, we focus on the most significant findings related to the structure, function, and diversity of styles in the Asteraceae family

STYLE CHARACTERS

In our comprehensive study of styles (Erbar & Leins, 2021) we presented the style morphology of more than 580 species of 346 genera covering all (presently accepted) 44 tribes of the Asteraceae, studied by SEM (each genus was at least presented by a SEM image) and, in selected examples, by histological sections. Our studies have shown that stylar features of the Asteraceae often cannot be discerned with a stereo microscope alone.

The comparison of style morphology results in the characterization of 49 style types (Fig. 1 in Erbar & Leins, 2021). We introduced a new possibility to visualize as many important style characters as possible in a diagrammatic presentation (Erbar & Leins, 2015). We use special side/front sketches of the style from shortly below the bifurcation up to the tips of the style branches (total length of the style is not recognized; see legend for Figure 2–Figure 5). These special diagrams are used in the compilations in Figure 2–Figure 5, where the style types are arranged according to the asignment to the different mechanisms of secondary pollen presentation.

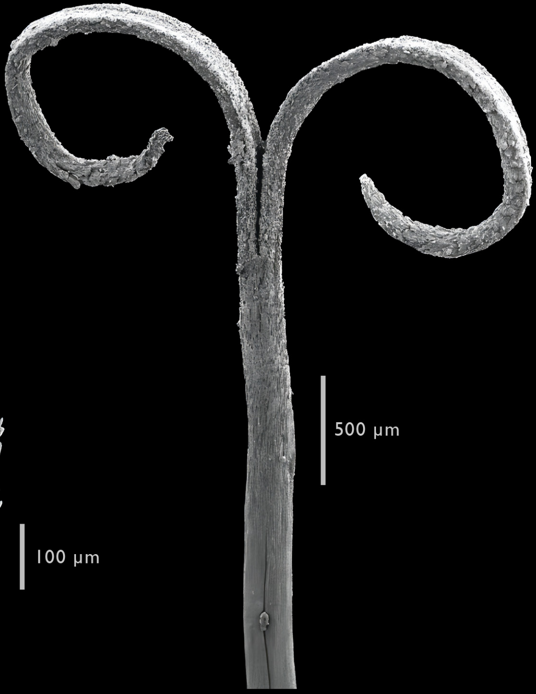
In this synopsis, we will not repeat the formalised description of the types detailed in Erbar & Leins (2021) but instead highlight essentials, sometimes in comparison to similar types although essentially maintaining the sequence of subfamilies and tribes.

Early-diverging subfamilies

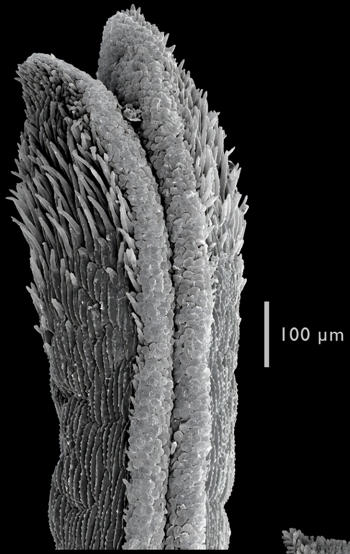
The ***Arnaldoa*-style type** (see page 2 and Figure 2) is characterized by a shortly bifid, papillate style and a continuous stigmatic tissue. The ***Schlechtendalia*-style type** (see page 2 and Figure 2) differs in that the lower end of the papillary zone is somewhat thickened. The shortly bifid styles of the ***Barnadesia* type** (see page 2 and Figure 4) are smooth. Each rounded style branch has a transverse bulge at its base and continuous stigmatic tissue. The glabrous styles of the ***Fulcaldea* type** (see page 2 and Figure 4) exhibit an ellipsoidal thickening distinctly

Trichome diversity in the basal grade

The shape and arrangement of style trichomes influence the mechanisms of secondary pollen presentation. In *Dinoseris* and *Wunderlichia*, bi- to multiseriate style trichomes permit only a deposition or simple brushing mechanism. In contrast, other styles participate in pump mechanisms.



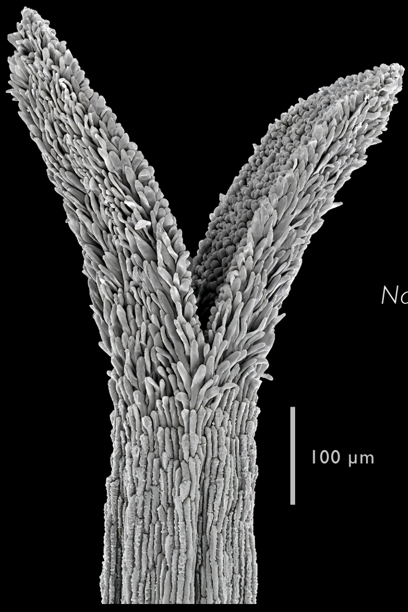
Dinoseris salicifolia
STIFFTIEAE



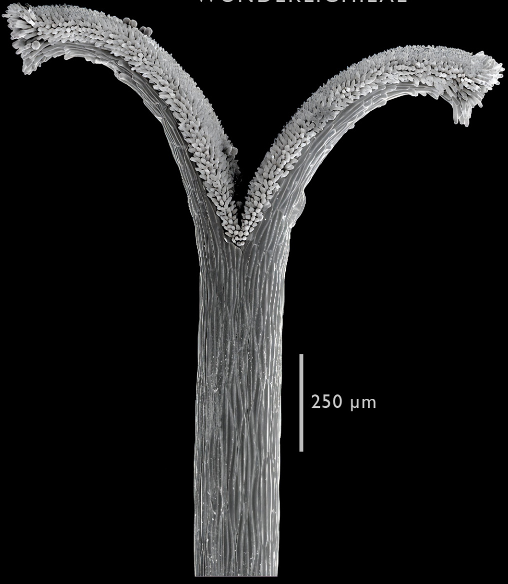
Onoseris odorata
ONOSERIDEAE

Wunderlichia mirabilis
WUNDERLICHIEAE

Nassauvia abbreviata
NASSAUVIEAE



Aphyllocladus spartioides
ONOSERIDEAE



Leucheria suaveolens
NASSAUVIEAE

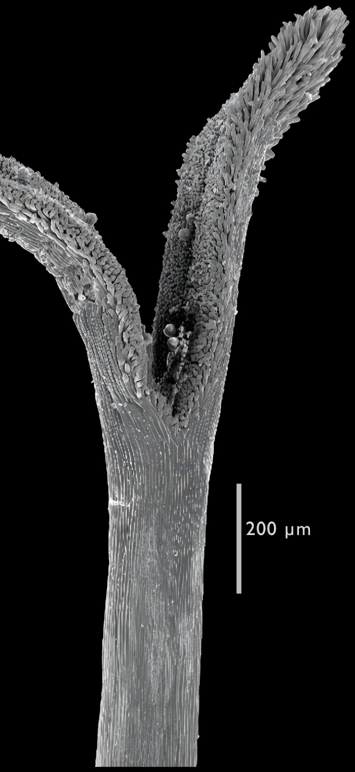
below its bifurcation. The ***Famatinanthus*-style type** (see page 2 and Figure 2) is unique with its indented epidermis (cobblestone-like epidermis units). The ***Stifftia*-style type** (see page 2 and Figure 4) is characterized by its rounded style branches somewhat thickened at their tips, rugulose due to protruding epidermal cell groups and a continuous stigmatic tissue. In the ***Dinoseris* type** (see page 4 and Figure 4), the rather long, slender styles are rugulose over their entire length (to somewhat below the bifurcation) by bi- to multiseriate style trichomes. Scale-like multi-seriate style trichomes occur in the ***Wunderlichia*-style type** (see page 4 and Figure 2), too. However, as a particular feature, the style branches adhere together by cell wall swelling of the median ventral tissue. Stigmatic tissue covers the entire **free** part of the inner surface of the style branches, i.e. except for the adhesion zone. *Aphyllocladus*- and *Onoseris*-style types do not differ so greatly in the style trichomes arrangement (in *Onoseris* type, the style trichomes are confined to the very tips of the style branches, whereas in *Aphyllocladus* type, style trichomes may cover almost the entire dorsal side of the style branches), but in the shape of the stigmatic area. In the ***Aphyllocladus*-style type** (see page 4 and Figure 5), the stigmatic tissue is continuous over the entire inner side of the style branches, whereas the ***Onoseris*-style type** (see page 4 and Figure 4) belongs to those style types, in which the stigmatic area becomes U-shaped. This happens by the median ventral tissues (i.e. a pollen tube transmitting tissue) of the style branches adhering proximally. Strictly speaking, the stigmatic tissue also covers the entire inner surface of the **free** part of the style branches. *Leucheria*- and *Nassauvia*-style types have distinctly bifid styles that are glabrous except for the very tips of their branches and stigmatic tissue covers their entire inner surface. In the ***Leucheria*-style type** (see page 4 and Figure 4), truncate style branches bear apically a tuft of trichomes, whereas in the ***Nassauvia*-style type** (see page 4 and Figure 4), acute style branches are apically provided with trichomes, which are longer at the base of the triangular apex than those ones at its dorsal surface. The styles of the ***Proustia* type** (see page 6 and Figure 5) differ in that the upper third of its style branches is covered with trichomes. In the ***Mutisia*-style type** (see page 6 and Figure 5), style trichomes cover the distal part of the (acute to subacute) style branches, too. Characteristic, however, is the stigmatic tissue arranged in two marginal bands that become confluent apically. Ventrally (between the receptive marginal bands), the inner stylar branch surface is covered with non-receptive (long) papillae (inversely U-shaped stigma on the inside of the style branches; see page 6). The ***Gochnatia*-style type** (see page 6 and Figure 4) is characterized by a stout, glabrous style that is dorsally, just beneath the apices of the short style branches, thickened. Stigmatic tissue covering the entire inner surface of the style branches projects apically and laterally forming a more or less prominent ridge.

Pertyoideae and Carduoideae

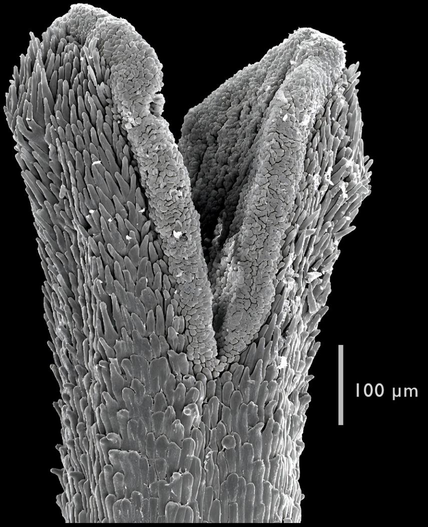
An inversely U-shaped stigma realized by the loss of receptivity of the papillate median tissue, as well found in the *Mutisia* type as described above (although unusual in the basal tribes), also characterises the ***Ainsliaea*-style type** (Figure 5). In *Ainsliaea* type, in contrast to *Mutisia* type, style trichomes extend from the apex of its rather short, rounded to truncate style branches to somewhat beneath the bifurcation. Styles of ***Oldenburgia* intermedia type** (Figure 4) and ***Oldenburgia papionum* type** (see page 6 and Figure 4) are rather thick with short, apically rounded style branches, thus resembling somewhat the *Gochnatia* type, but differ from it and from each other by the occurrence of trichomes. Common to all three types is a dorsal swelling beneath the apex of each stylar branch. In *Oldenburgia intermedia* type, the surface of the style branches is glabrous but with some papillae apically, in *O. papionum* type, the style is papillate-hairy from the apex of the style branches to somewhat below the bifurcation with even some longer, acute trichomes apically. Both *Oldenburgia*-style types differ from the *Gochnatia*-style type primarily by the arrangement of the stigma (two stigmatic marginal bands confluent apically in *Oldenburgia* type versus stigmatic tissue covering the entire inner surface of the style branches in *Gochnatia* type). In the stigma arrangement both *Oldenburgia* types resemble the *Ainsliaea* type. The style of the ***Dicoma* type** (Figure 4) is distinctly bifid, with a short-pilose distal part of its style branches and long style trichomes forming a subapical tuft beneath the pilose area. The median ventral tissues of the style branches adhere proximally, resulting in stigmatic tissue confined to the very distal area and the peripheral areas next to the adhesion

Variation in style surface and hair arrangement in early diverging clades: endless diversity

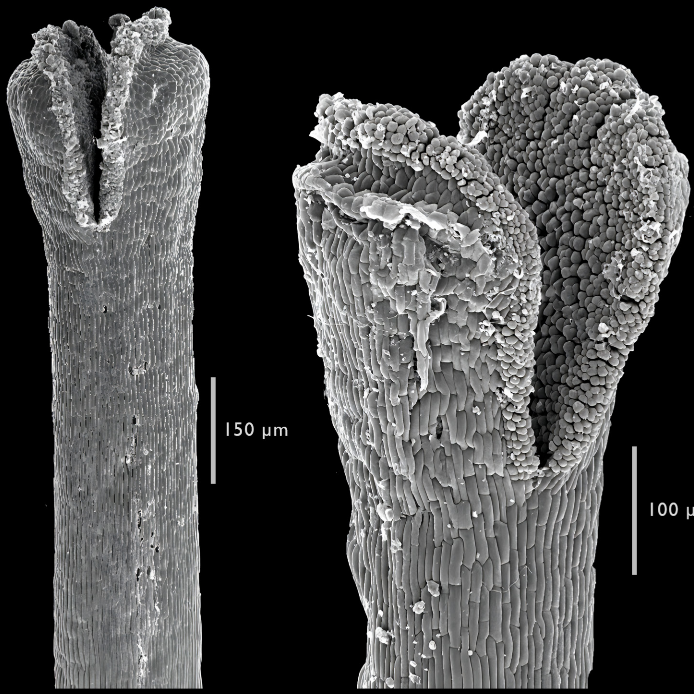
The substantial styles with apically rounded (*Oldenburgia*) or thickened (*Gochnatia*) style branches are well-suited for a pump mechanism in secondary pollen presentation. In *Mutisia* and *Proustia*, trichomes located on the upper part of the style branches facilitate the brushing out of pollen grains, enhancing the efficiency of the pump mechanism, which initially causes pollen to protrude from the anther tube.



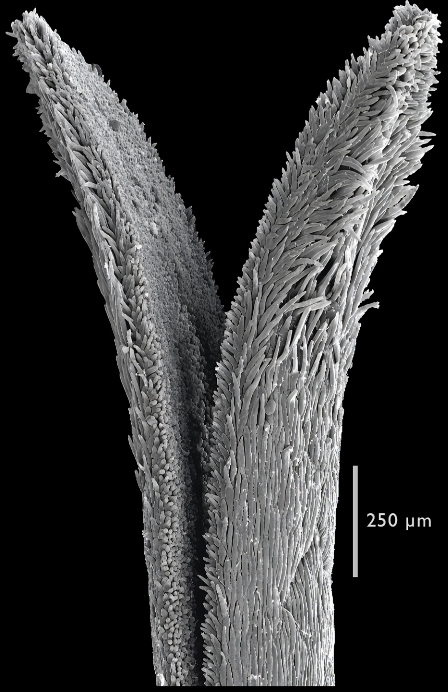
Proustia pyrifolia
NASSAUVIEAE



Oldenburgia papionum
OLDENBURGIEAE



Gochnatia foliolosa
GOCHNATIEAE



Mutisia acuminata
MUTISIEAE

zone. ***Macledium/Cyanus***, ***Arctium***, ***Centaurea***, ***Carduus***, and ***Staehelina* types** (see page 9 and Figure 5) are characterized by a distinct collar of trichomes – either directly beneath the style branches (as in *Macledium/Cyanus*-, *Centaurea*- and *Staehelina*-style types) or further down on the stylar shaft (as in *Arctium*- and *Carduus*-style types). *Macledium/Cyanus*- and *Arctium* types show a continuous stigmatic area, whereas in *Centaurea* and *Carduus* types the median ventral tissues (i.e., a pollen tube transmitting tissue) of the style branches adhere proximally so that stigmatic tissue is confined to the very distal area and the peripheral areas next to the adhesion zone; the stigmatic margins fold back at late anthesis when stigma is receptive. In the *Staehelina* type, the stigmatic tissue is arranged in two marginal stripes that are confluent apically, ventrally between the receptive marginal bands the inner stylar branch surface is covered with non-receptive papillae. In *Centaurea* L. species, style branches and adhesion zone differ in length (compare *C. scabiosa* L. and *C. sphaerocephala* L., see page 9). Styles of the ***Berardia*** and ***Cousinia* types** (Figure 5) share stigmatic tissue covering the entire inner surface of the style branches, but differ in size and arrangement of style trichomes. In the *Berardia*-style type, style trichomes extend from below the stylar tips distinctly beneath the bifurcation. In the *Cousinia*-style type the style trichomes on the branches and the shaft are disorderly scattered, some longer ones are observable in the region beneath the bifurcation, shorter ones extend well onto the stylar shaft.

Vernonioideae, Cichorioideae, and Corymbioideae

The ***Arctotis*-style type** (see page 9 and Figure 3) is easy to identify by its barrel-shape and the collar of long trichomes at the base of this thickened apical part. Stigmatic papillae cover the entire inner surface of style branches. ***Vernonia* type** (see page 9 and Figure 3) and ***Cichorium* type** (Figure 3) share distinctly bifid, slender styles that are evenly pilose along the style branches and a large part of the stylar shaft (hairy zone usually considerably extending beneath the bifurcation point). Whereas in the *Cichorium* style type stigmatic tissue covers the entire inner surface of the style branches from the stylar tip to the bifurcation point, the uppermost part of the style branches is free of stigmatic papillae (but covered with style trichomes). The **Corymbium-style type** (see page 11 and Figure 3) differs from the *Cichorium* type in that the hairy part of the stylar shaft is somewhat thickened.

Asteroideae

Stigmatic tissue arranged in two discrete lateral lines (sometimes broad stigmatic bands nearly touch each other, but at least one sterile cell line inbetween) characterizes the *Anthemis/Senecio*-, *Jacobaea***-**, *Aster*-, *Madia*-, *Gynura*-, *Gaillardia*-, *Cosmos*-, and *Eupatorium*-style types. Differences exist in the shape of the stylar branch tips and in the arrangement of style trichomes. In the ***Anthemis/Senecio* type** (see page 11 and Figure 4), the truncate, obtuse or conical style branches are glabrous except for the very tips of its style branches: (sub)apically they are provided with a tuft of trichomes. Styles of the ***Jacobaea* type** (Figure 5) feature, in addition to the (sub)apical tuft of trichomes, shorter trichomes distributed dorsally along the branches. These trichomes extend from approximately one-third of the branch's length to its entire length, with their density and length gradually decreasing toward the proximal end. *Aster-, Madia*-, *Gynura*-, *Gaillardia*-, *Cosmos*-, and *Eupatorium*-style types are characterized by stylar branch appendages that may be very specialized. The glabrous style branches of the ***Aster* type** (see page 28 and Figure 5) generally have hairy acute appendages, triangular (or oblong) in shape (in their style, the North American *Symphyotrichum* species, formerly placed among the asters, and the European asters match). In the ***Madia* type** (Figure 5), the hairy style branches exhibit narrowly triangular appendages. Long, gradually tapering appendages provided with long, obtuse, sometimes clavate trichomes that are loosely scattered over the appendages are characteristic for styles of the ***Gynura* type** (see page 11 and Figure 3). In the ***Gaillardia* type** (Figure 5), the linear, tapering appendages of the style branches that are much longer than the stigmatic area and have a tuft of longer trichomes at the base of the hairy appendage are most distinctive. The ***Cosmos* type** (see page 11 and Figure 5) is characterized by a hairy triangular stylar branch appendage, whose tip is markedly defined. The ***Eupatorium* type** (see page 13 and Figure 3) is clearly recognisable by enlarged papillate-pilose stylar branch appendages (filiform, lanceolate or clavate, sometimes slightly broadened or flattened distally) above the stigma-bearing area that is mostly shorter than the appendages. The last eleven style types exhibit apically confluent stigmata (inversely U-shaped stigmata). ***Doronicum***, ***Dimorphotheca***, and ***Ligularia* types** (see page 13, Figure 4, and Figure 5) share truncate to sligthly obtuse style branches with an apically (or subapically) tuft of trichomes. In *Doronicum* and *Dimorphotheca* types, the styles are glabrous except for the very tips of their style branches, whereas in the *Ligularia* type, additionally to the tuft of trichomes, shorter trichomes are found dorsally over the entire stylar branch length. In the *Doronicum* and *Ligularia* types, stigmatic tissue is continuous over a major portion of the inner surface (apart from a small proximal area), in the *Dimorphotheca* style the stigmatic tissue is arranged in two discrete lateral lines confluent apically. The ***Osmitopsis* type** (see page 13 and Figure 4) shares with the *Doronicum* and *Ligularia* types the arrangement of the stigmatic tissue, but the style branches are truncate with an apical small tuft of trichomes. A distinctive feature is the presence of large-headed glands on the style. ***Adenostyles***, ***Garuleum***, ***Inula***, ***Blumea*** and ***Pluchea* style types** (see page 13, page 14, Figure 3, and Figure 5) share subacute to rounded stylar branch tips and style trichomes that extend beyond the tips. In *Adenostyles*, *Garuleum*, *Blumea*, and *Pluchea* types, style trichomes even cover the entire length of the style branches, extending to their base or even just beneath the bifurcation (in *Blumea* and *Pluchea* style types trichomes rounded to blistered and more or less densely packed). The styles of the *Inula* type are glabrous except for the distal part of its rounded, sometimes apically somewhat broadened style branches (style trichomes not reaching the bifurcation). The *Inula* type shares with the *Adenostyles* and *Blumea* types that the stigmatic bands run parallel to each other before they are confluent apically (near the stylar branch tip). In the *Garuleum* and *Pluchea* types, the stigmatic bands are separated only over a short distance; the stigma is continuous over the largest part of the stylar branch. Triangular to oblong hairy stylar branch appendages and hairy zones extending halfway down their style branches characterize the ***Calea*** and ***Helianthus* type** (see page 14, and Figure 5). In the *Calea* type, the stigmatic tissue is arranged in two distinct lateral lines that converge subapically but remain confined to a narrow band. In the *Helianthus* type, the "confluent zone" is so extensive that the stigmatic tissue covers most of the inner surface, leaving only a more or less wedge-shaped proximal area devoid of receptive papillae. Notably, in *Helianthus* species, these non-receptive areas vary in size. Unlike all other style types with apically confluent stigmatic areas, the outermost tip of the inner surface of the style branches in both the *Calea* and *Helianthus* types is free of stigmatic papillae.

The value of style characters for more detailed phylogenetic considerations – just a few remarks

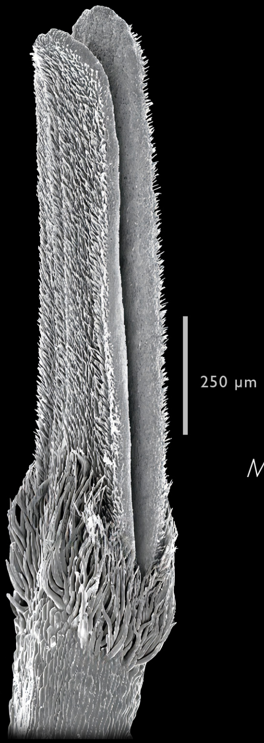
Plotting our style types onto a modern phylogenetic tree as reference (Figure 1), we can find astonishing correspondences in several clades, but also deviations in others; the latter showing e.g., parallelisms. Nevertheless, the whole family can be divided into four groups with regard to style types (for a detailed discussion and references see Erbar & Leins, 2021).

The "basal" (i.e., early-diverging) subfamilies Barnadesioideae, Famatinanthoideae, Stifftioideae, Mutisioideae, Wunderlichioideae, Gochnatioideae, and Hecastocleidoideae: Apart from the *Mutisia*-style type (Figure 5), the other 14 style types established for this group are confined to these subfamilies (yellow squares in Figure 1). In addition, the *Adenostyles*-style type (Figure 5)occurs in the African members of the Mutisieae; this style type is otherwise only found in Asteroideae. The high diversity of stylar shapes within the seven subfamilies, which represent only about 3% of the species of Asteraceae, is remarkable. Styles are completely smooth or sub-papillate or hairy. The *Gochnatia*-style type, which is the most frequent one, occurs in several clades. Two tribes (Barnadesieae and Nassauvieae) are characterized by several style types, which, however, do not occur in the other tribes. *Onoseris*- and *Wunderlichia*-style type are characterized by an adhesion zone of the median ventral tissues of the inner surface of the style branches. Apart from the basal subfamilies, adhesion zones are only found in three style types within the Carduoideae (*Dicoma*-, *Centaurea*-, *Carduus*-style type). The monotypic genus *Famatinanthus* exhibits with its cobblestone-like surface a unique style type, supporting the elevation to tribe and subfamily rank due to *cpDNA* data (Panero et al., 2014).

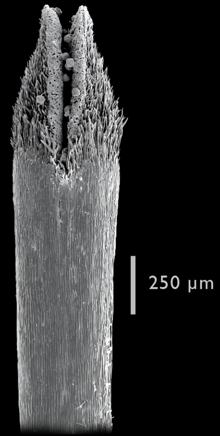
Pertyoideae and Carduoideae: The eleven style types established for these two subfamilies

Distinctive features: collar versus long hairy branches and shaft

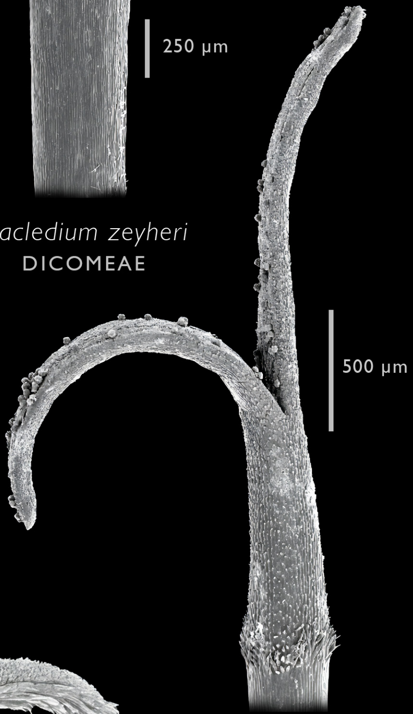
The five carduoid style types are distinguished by a prominent collar of trichomes located at various positions along the style shaft, facilitating a specialized pump mechanism for secondary pollen presentation. In *Arctotis*, the entire pollen output is displayed on the pilose, barrel-shaped stylar region, exemplifying a unique brushing mechanism. Long, filiform style branches with sweeping trichomes extending below the bifurcation point characterize the styles of Cichorieae and Vernonieae. The distinction lies in the arrangement of the stigmatic papillae: in the *Vernonia* type, the stigmatic papillae do not extend to the uppermost part of the style branches.



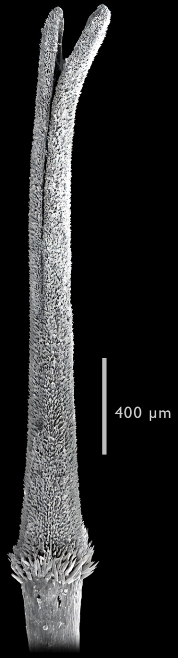
Centaurea sphaerocephala
CARDUEAE



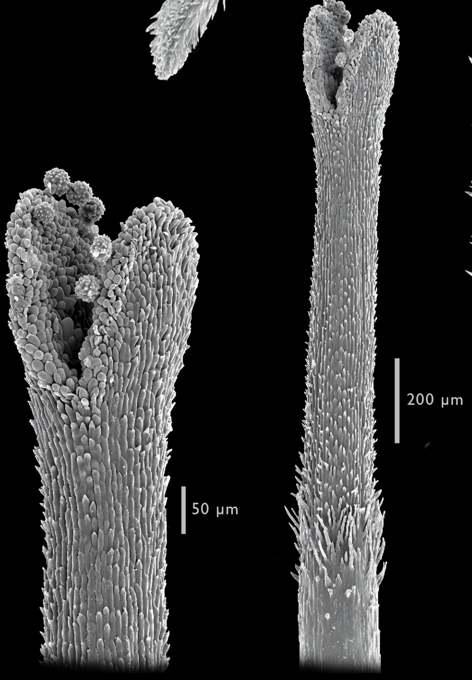
Macledium zeyheri
DICOMEAE



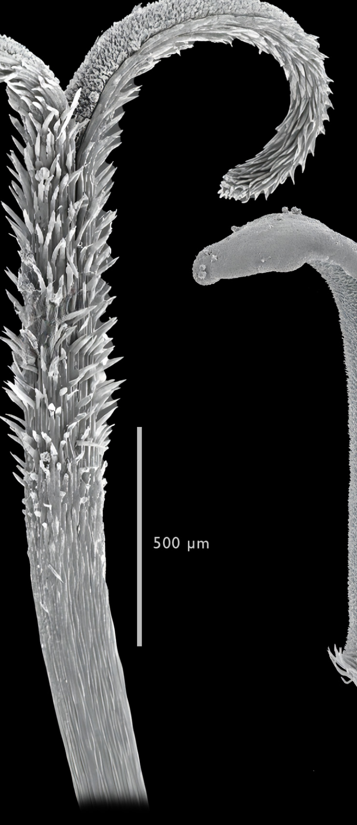
Arctium tomentosum
CARDUEAE



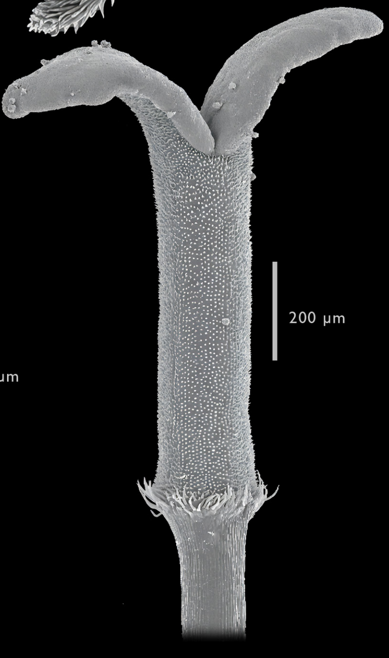
Carduus defloratus
CARDUEAE



Staehelina dubia
CARDUEAE



Vernonia noveboracensis
VERNONIEAE



Arctotis venusta
ARCTOTIDEAE

(purple squares in Figure 1) are not found in other subfamilies. Five of them are characterized by a collar of long style trichomes, either at or distinctly beneath the bifurcation point.

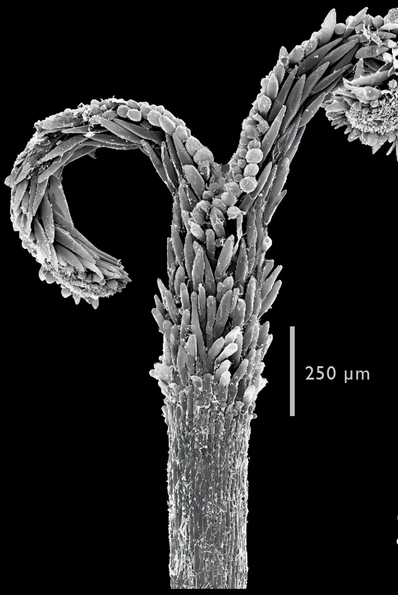
The adhering of the style branches can be used to distinguish two related genera, namely *Centaurea* L. and *Cyanus* Mill. In *Cyanus*, the style branches are separate and divergent, whereas they adhere to each other for most of their length (mediated by their median ventral tissues) in *Centaurea* (see page 9). *Cousinia* Cass. (about 600 species) is the largest genus of the tribe Cardueae and one of the largest of the whole Compositae. We cannot confirm that the *Cousinia* style resembles the vernonioid style type sensu Bremer (1987, 1994), in which the sweeping trichomes are all of equal length and extend well below the bifurcation as stated in the literature. We observed that long, slender trichomes are disorderly scattered along the style branches and shorter trichomes extend well onto the stylar shaft; some longer trichomes are found in the region beneath the bifurcation, thus suggesting a not well-developed collar of trichomes. Thus we established a style type of its own for *Cousinia* (Figure 5).

Vernonioideae, Cichorioideae, and Corymbioideae: The four style types (red squares in Figure 1) occurring in these subfamilies are confined to them. The prevailing style types (*Vernonia* and *Cichorium* type, see page 9) differ only by the fact that in the *Vernonia* type the continuous stigmatic tissue does not reach the uppermost part of the inner surface of the style branches; instead, this uppermost part is covered with style trichomes. Although the difference in the extent of the stigmatic tissue is small, the occurrence of the two style types matches the new delimitation of subfamilies Vernonioideae and Cichorioideae (Mandel et al., 2019). Only the narrowly defined Cichorioideae. exhibit the long, filiform styles with the stylar branch inner surfaces completely covered by stigmatic papillae (Figure 3).

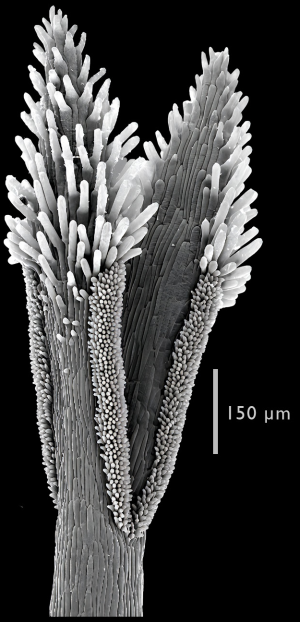
Asteroideae: The subfamily is a well-defined group (both morphologically and molecularly) and contains about 62% of the species in the family (about 15,500 species in a total of about 1,230 genera; Pelser & Watson, 2009). The largest and most widely distributed tribes are the cosmopolitan Astereae and Senecioneae. The 20 tribes presently accepted in the large subfamily Asteroideae are categorized in three main lineages recognized as supertribes Senecionodae, Asterodae, and Helianthodae. Of the 20 style types occurring in this largest subfamily, 18 of them are confined to this group (orange squares in Figure 1). Most of the styles have either truncate to slightly obtuse style branches with a (sub)apical tuft of trichomes or style branches with hairy, triangular or oblong appendages. The arrangement of the stigmatic tissue in two small ventro-marginal bands is common in the Asteroideae and, important to emphasize, restricted to this subfamily (see page 24). However, further arrangements can be found: broad stigmatic bands, nearly touching each other, or separate lines become apically confluent. In a few instances, the stigmatic tissue seems to cover the whole inner surface. Detailed investigations, mainly by histological cross sections, reveal that there is at least one sterile cell line in the middle of the inner stylar branch surface or a small wedge-shaped sterile area at the proximal end of the stylar branch (Erbar & Leins, 2016).

Senecionodae (with only tribe Senecioneae) exhibit six style types, five of which are restricted to the Asteroideae and one (*Gynura* type) is only found in this tribe. Only the *Adenostyles* type is found in a basal group (*Gerbera* L., *Perdicium* L., Mutisieae). *Senecio* sect. *Jacobaea* and *Senecio* s.str. form two clades that are only distantly related (DNA sequence data, Pelser et al. 2002). As regards style characters, we distinguish two style types. The typical senecioid style, as usually referred to in the literature, is two-branched with two parallel stigmatic bands on the inside, and the glabrous style branches are truncate with (sub)apical sweeping trichomes. This corresponds to our *Anthemis*/*Senecio*-style type (Figure 4). More often we found the *Jacobaea*-style type (Figure 5), which differs by having trichomes not only in the (sub)apical tuft of trichomes, but shorter trichomes extending dorsally along the branches (about third of the branch up to its entire length, density and length of the trichomes decreasing proximally). Both style types occur outside the Senecioneae (see red squares with numerals 32 and 33 in Figure 1).

The four tribes of Asterodae exhibit nine different style types. Three of them are restricted to a single genus (*Dimorphotheca* type #38, *Garuleum* type #37, *Osmitopsis* type #40). The large tribe Astereae is moderately diverse in style morphology.

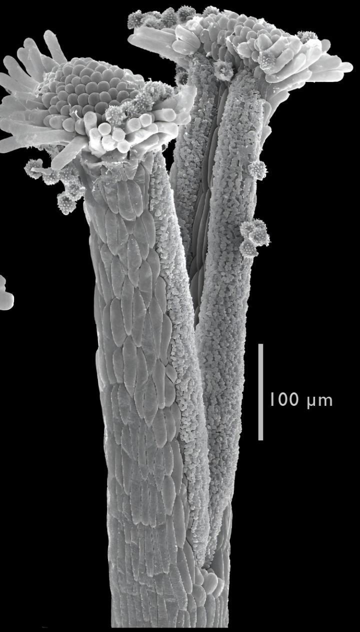


Corymbium africanum
CORYMBIEAE



Symphyotrichum dumosum
ASTEREAE

Anthemis maritima
ANTHEMIDEAE



Senecio vernalis
SENECIONEAE

Style branch appendages in Asteroideae: to be, or not to be

Style branch tips exhibit various morphologies across different genera. In *Corymbium*, they taper to a point, while in *Anthemis* and *Senecio*, they are truncate and feature an apical tuft of trichomes. Some species possess distinct appendages: *Symphyotrichum* displays acute triangular, hairy appendages; *Cosmos* has triangular appendages with a well-defined tip; and *Gynura* presents long, gradually tapering appendages with sparsely distributed trichomes.

Gynura splendens
SENECIONEAE

Cosmos bipinnatus
COREOPSIDEAE

Most members, however, are characterized by one type, namely the *Aster*-style type. Anthemideae, in contrast, are uniform throughout (apart from *Osmitopsis*).

Supertribe Helianthodae (15 tribes exhibit 16 different style types), the largest of the three supertribes of Asteroideae, is dominated by the so-called "Heliantheae alliance" (12 tribes exhibit 11 different style types) sensu Panero (2007) that contains about 5500 species or about 20%–25% of the species recognized in Asteraceae, including sunflowers (*Helianthus* L. , sneezeweeds (*Helenium* L.), tarweeds (*Madia* Molina), and eupatoriums (*Eupatorium* L.). Any obvious systematic pattern in the distribution of these style types is absent. In addition, variability in style types does not correlate with the tribe size. Five different style types are found in the moderately large tribe Inuleae as well as in the large tribe Heliantheae. In the largest tribe within Helianthodae and one of the largest tribes in Asteraceae, namely Eupatorieae, only one style type occurs that is moreover rather distinct from all other types.

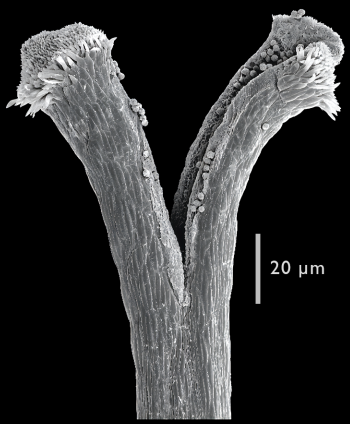
Concerning Asteroideae as a whole, again, no obvious systematic pattern in the distribution of style types becomes obvious. Twenty style types are found in the twenty tribes (Figure 1). From outside the Asteroideae, only the *Mutisia* type is found (in Helenieae). Apart from the *Adenostyles* type, all other style types are confined to the Asteroideae. Only three style types occur in all three supertribes: the *Anthemis*/*Senecio* type (in six tribes), the very similar *Jacobaea* type (in three tribes) and the *Aster* type (in four tribes). Style types with separate parallel stigmatic lines characterize seven types, but style types with apically confluent stigmata (inversely U-shaped stigmata) as well as almost continuous stigmata (only proximally a small, wedge-shaped area of sterile tissue) are found.

Concerning Asteraceae as a whole (Figure 1), there are only two "outliers", i.e., style types occurring in two of the four groups mentioned, namely the *Mutisia* and *Adenostyles* types (see page 6, page 13, and Figure 5). The *Mutisia* type occurs in the Mutisieae investigated (except for *Mutisia coccinea* A.St.-Hil.), in two genera of the Inuleae (i.e., *Calostephane* Benth., *Pegolettia* Cass.) and in one genus of the Helenieae (i.e., *Pelucha* S.Watson). Within the Asteroideae, the *Adenostyles* type occurs in Senecioneae, Astereae, and in the Inuleae. Thus, Mutisieae and Inuleae are the two tribes, where these style types occur side by side. Both style types are relatively similar; they match the stigma arrangement, but differ in the stylar hair arrangement, namely style trichomes positioned in the distal part of the style branches (*Mutisia* L.f.) versus hairy zone extending to the base of the branches or just beneath the bifurcation (*Adenostyles* Cass.). In addition, they differ in the shape of the style trichomes. They are obtuse in the *Adenostyles* type (as common in the Asteroideae) and more or less acute in the *Mutisia* type (in the early-diverging groups rounded as well as acute style trichomes are found). The different hair arrangement is the key factor in determing the relative involvement of pumping and brushing in secondary pollen presentation (see chapter on secondary pollen presentation).

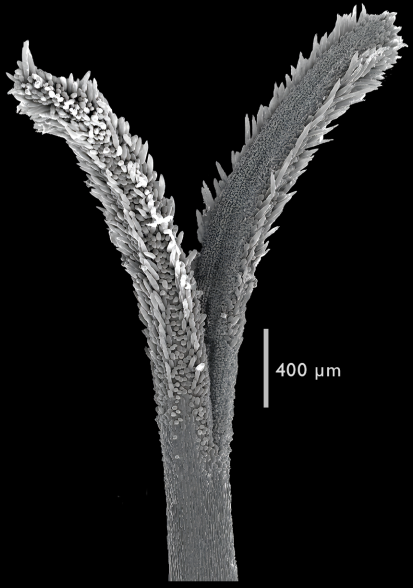
STYLE TYPES AND SECONDARY POLLEN PRESENTATION

We were interested in the styles especially with regard to their function in secondary pollen presentation (e.g., Leins & Erbar, 1990, 2006, 2010). In secondary pollen presentation, covering different portioning mechanisms, pollen is relocated from the anthers (the place of their origin) onto another floral structure, as the flower is still unopened. In all Asteraceae, it is the style that is involved in secondary pollen presentation. In bud stage, the introrse anthers open inwards, releasing the pollen grains into the anther tube (in addition to the capitulum inflorescence, the anthers adhering in a tube characterizes the family throughout). An elongating style pushes and/or brushes the pollen out of the anther tube. It is mainly the arrangement of the style trichomes that is correlated to a function in the process of secondary pollen presentation. After detailed studies, we assigned the 49 style types to one of the mechanism of secondary pollen presentations (see Figure 2–Figure 5); for a more detailed discussion see Erbar & Leins (2021). The mechanisms differ in the absence or presence of style trichomes, in the length of a hairy zone and in the position of the stylar tip at anther dehiscence. Pure pump and brushing mechanisms are easily

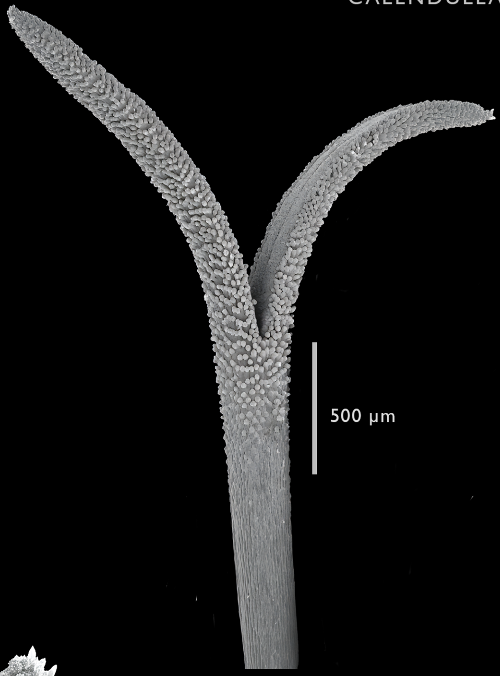
Eupatorium cannabinum
EUPATORIEAE



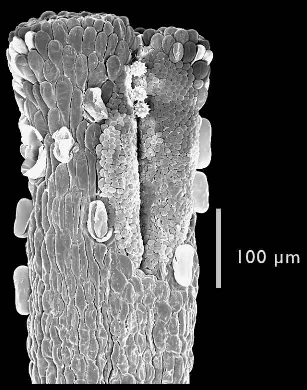
Dimorphotheca cuneata
CALENDULEAE



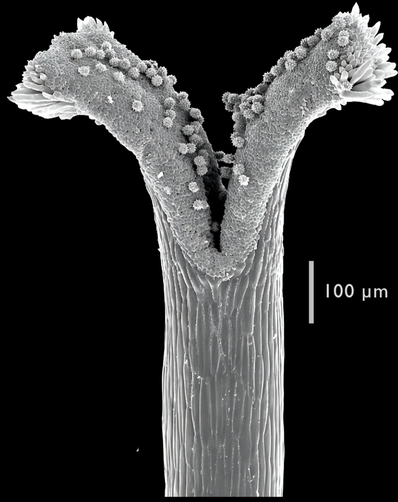
Ligularia dentata
SENECIONEAE



Adenostyles alliariae
SENECIONEAE



Osmitopsis asteriscoides
ANTHEMIDEAE



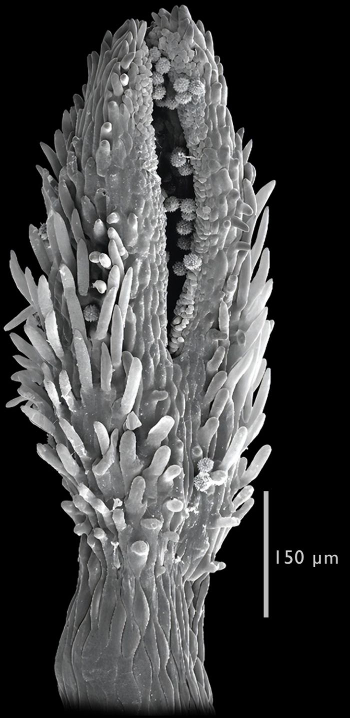
Doronicum hungaricum
SENECIONEAE

Unique styles in Asteroideae

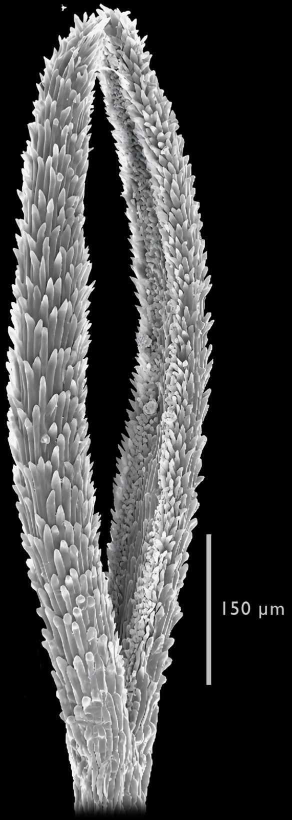
The *Doronicum* and *Ligularia* style types are present in two tribes, while the Eupatorium type is exclusive to the Eupatorieae. The *Dimorphotheca* and *Osmitopsis* types are characteristic of specific genera; notably, *Osmitopsis* is distinguished by its prominent glandular structures. The *Adenostyles* type exhibits an unusual distribution, occurring in both the Mutisieae and certain tribes within the Asteroideae.

A frequently overlooked trait in Asteroideae: apically confluent stigmata

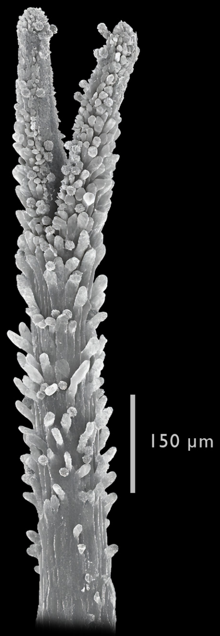
Within the Asteroideae, 11 distinct types exhibit variation in the size of the confluent zone. In the *Inula* and *Blumea* types, the confluent zone is restricted to the upper portion of the style branch, characterized by a long furrow of non-receptive cells separating discrete lateral stigmatic lines. In the *Garuleum* and *Pluchea* types, the lateral lines converge apically into a broad band, leaving only a small, wedge-shaped area proximally free of stigmatic papillae. In the *Calea* and *Helianthus* types, the uppermost tip, located above the confluent band, remains devoid of stigmatic papillae.



Garuleum schinzii
CALENDULEAE

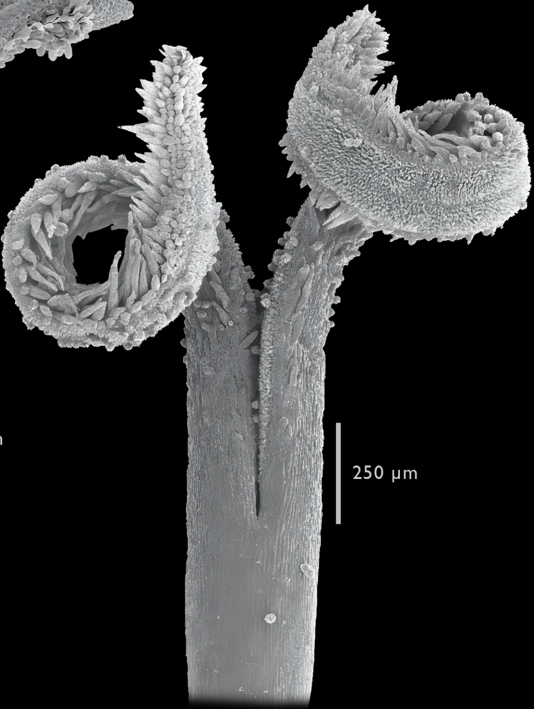


Blumea gariepina
INULEAE

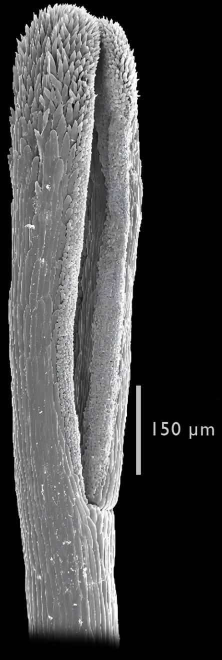


Pluchea chingoyo
INULEAE

Calea cymosa
NEUROLAENEAE



Helianthus annuus
HELIANTHEAE



Inlua helenium
INULEAE

STYLE TYPES
Across COMPOSITAE

🟨 Style types (1–15) of the basal (early-branching) groups, only type 13 also found in Asteroideae

🟪 Style types (16–26) of Pertyoideae and Carduoideae

🟥 Style types (27–30) of Vernonioideae, Cichorioideae, and Corymbioideae

🟧 Style types (31–49) of Asteroideae, only type 35 found in Mutisieae

⬜ Staminate flowers

A. Club-shaped styles with papillae or trichomes. **B.** Pestle-shaped styles with a subapical tuft of trichomes. **C.** Pestle-shaped styles with an apical tuft of trichomes. **D.** Deeply branched terete styles with trichomes. **E.** Unbranched terete styles with trichomes.

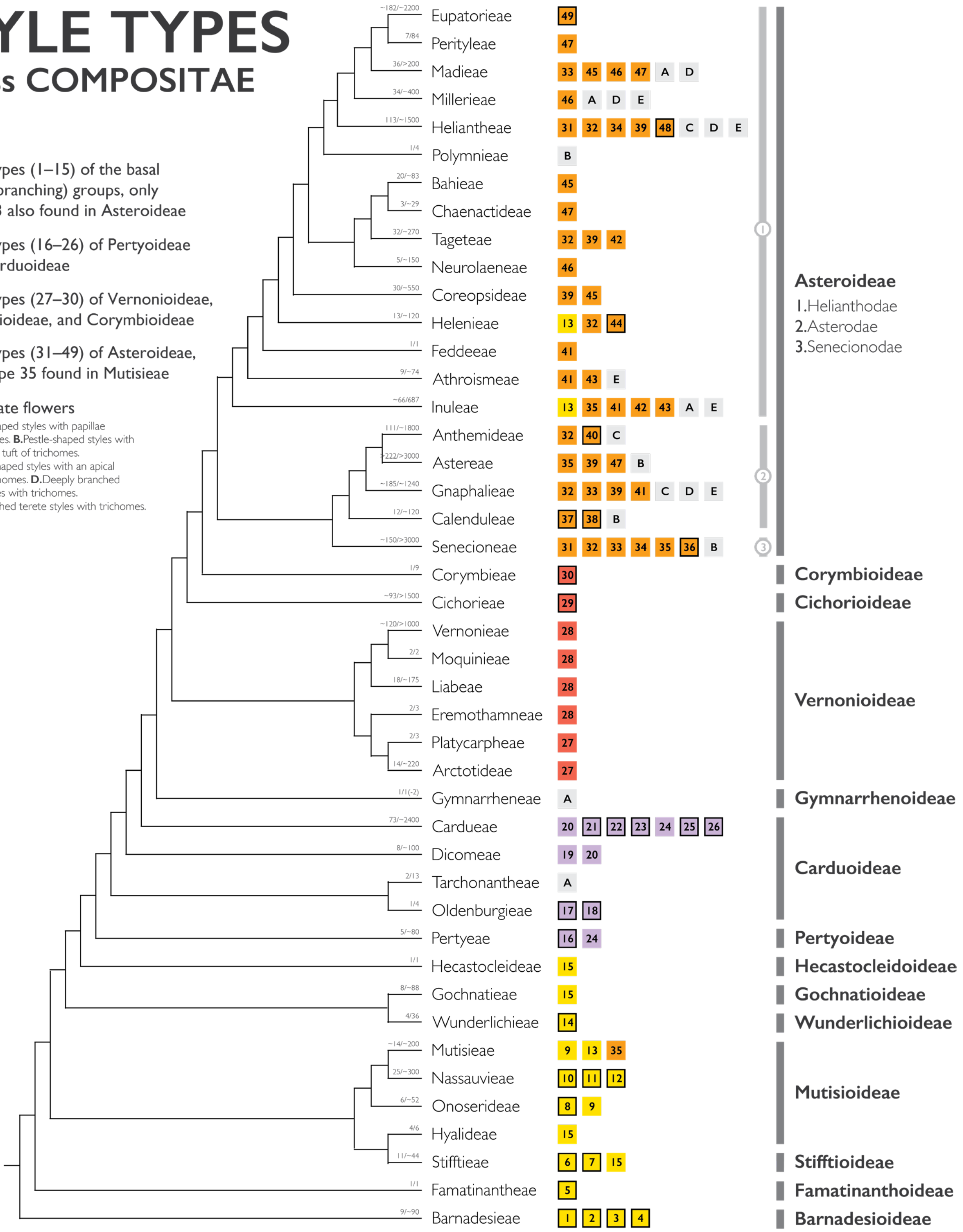


Figure 1. A generalized phylogenetic tree of Asteraceae (based on Funk et al., 2009b; Panero et al., 2014; Mandel et al., 2019) onto which the different style types are plotted. Only two style types occur in a basal tribe and in Asteroideae: type 13 (*Mutisia* type) in Mutisieae as well as in Inuleae and Helenieae, type 35 (*Adenostyles* type) in Senecioneae, Astereae, and Inuleae as well as Mutisieae; black outlined symbols: style type confined to the corresponding tribe.

distinguishable by the arrangement of the style trichomes: style trichomes only at the very tips of the style branches versus styles with a long hairy part. There are, however, more possibilities of pollen presentation in the Asteraceae. A pump and a brushing mechanism can be combined, a deposition mechanism as well as combinations of deposition and brushing occur. In addition, pump and brushing mechanisms can be modified to become different from the common type.

Deposition, brushing, pump and their combinations and variations are categorized into eight mechanisms (Figure 6–Figure 13): deposition/simple brushing mechanism, brushing mechanism, pump mechanism (with blocking trichomes), pump mechanism (with apical thickening), special pump mechanism, special brushing mechanism, combination of pump and brushing mechanism, combination of pump and slightly brushing mechanism. The most important preconditions and preadaptations, respectively, for all mechanisms include: radial symmetry of the flower bud, existence of a complete androecial whorl in a flower (i.e., five stamens), more or less long introrse anthers united by the coherence of their cuticles into a tube, protrandry of the flower the release of pollen occurs prior to the receptivity of the stigmatic surface). All mechanisms share three sequential processes before and/or during anthesis: 1. elongation of the filaments or stamen-corolla tube or both before the anthers open to bring these into the right position; 2. opening of the anthers, discharge of the pollen grains into the anther tube; 3. elongation of the style, by this presenting the pollen grains to the pollinating agent (see, e.g., Leins & Erbar, 2006, 2010).

In the **deposition/simple brushing mechanism** (Figure 6), the anther tube surrounds the style in bud stage. Just before the opening of the anthers, it only needs a moderate elongation of the filaments or stamen-corolla tube so that the long anther tube is level with the long papillate part of the style. After the deposition of the pollen grains onto the style, these are then carried out of the anther tube by stylar elongation and presented to the pollinators on the outside of the style. As with all other mechanisms, the style branches later on separate to expose the stigmatic surface. The rounded flat papillae or scale-like bi- to tri-seriate style trichomes (Figure 2) are not suitable for efficient sweeping. But the capturing of pollen grains may be assisted by abundant pollenkitt, by which the pollen grains adhere to the style Figure 6C). *Arnaldoa macbrideana* Ferreyra (Barnadesieae) is an example of the mechanism.

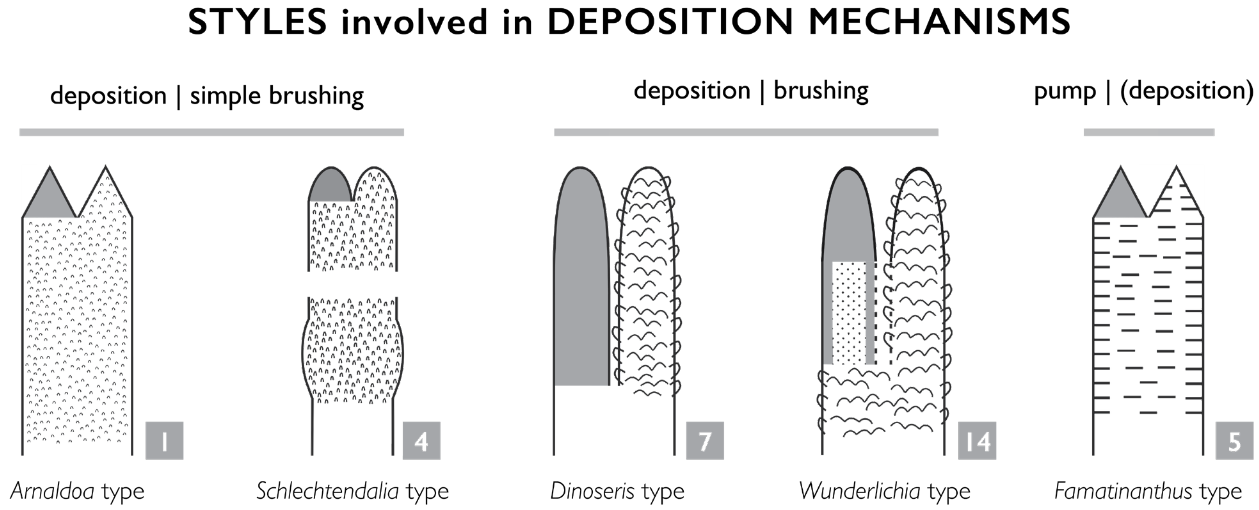
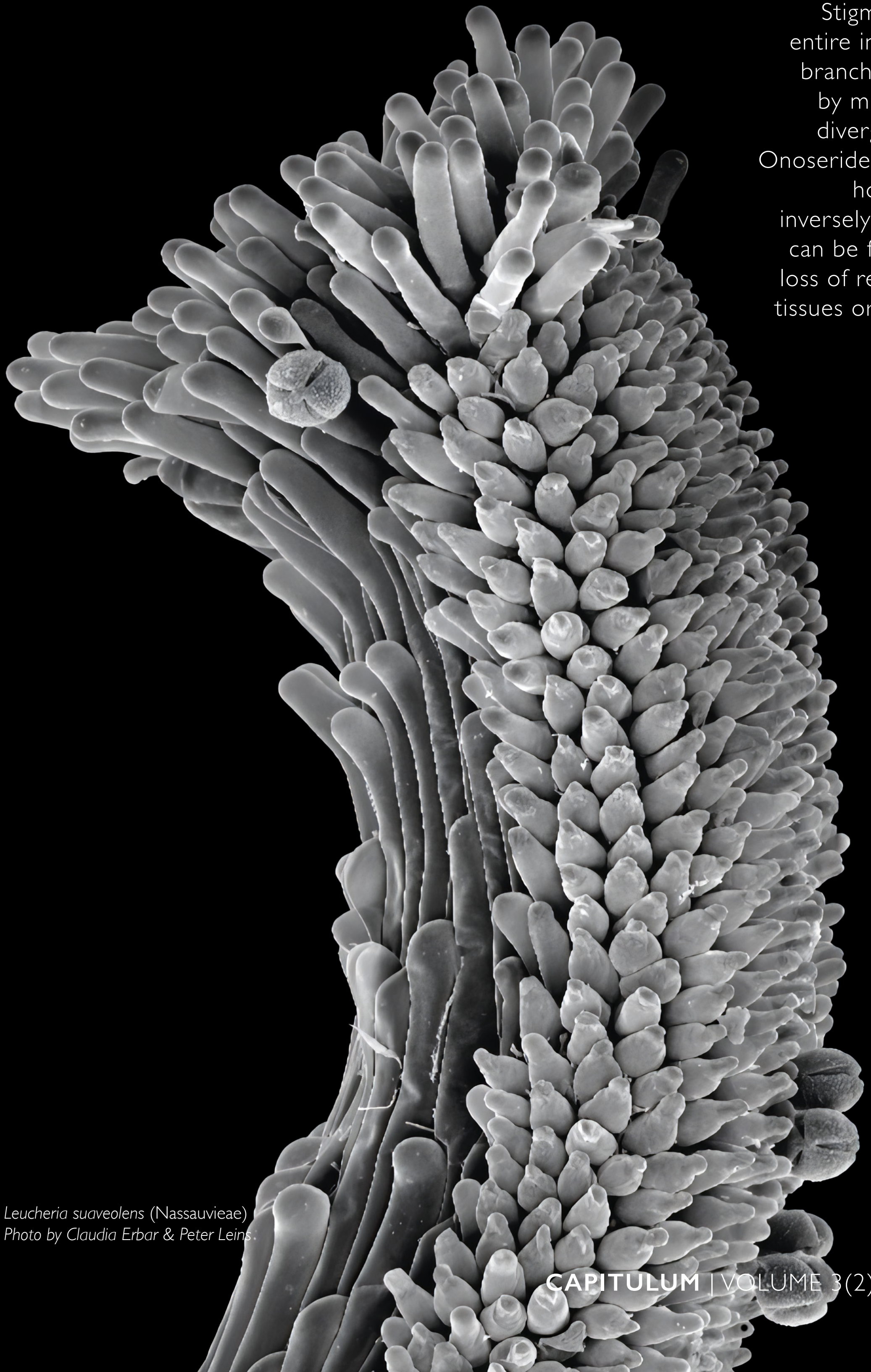


Figure 2. Compilation of style types involved in deposition mechanisms. The numerals correspond to the style type numbering in Erbar & Leins (2021). Illustrations feature single-plane diagrams rather than perspective drawings. The style branches are rotated 90° and flipped open, allowing both the adaxial (ventral, left) and abaxial (dorsal, right) views to be displayed in the same diagram. Variations in the length of the style branches are only approximated in the illustrations, and additional stylar parts are not depicted. The stigmatic tissue is shaded in grey, and any adhesion zone, if present, is indicated with dotted markings. Dorsal protrusions, as observed in the *Barnadesia*, *Gochnatia*, and both *Oldenburgia* style types, are shifted into a transverse plane, positioned on the left and right sides of the style branches.

A continuous field of stigmatic papillae

Stigmatic tissue covering the entire inner surface of the style branches is a character shared by most species in the early-diverging tribes. In Mutisieae, Onoserideae, and Wunderlichieae, however, a quite different inversely U-shaped arrangement can be found, realized either by loss of receptivity of the median tissues or by median adhesion of the style branches.

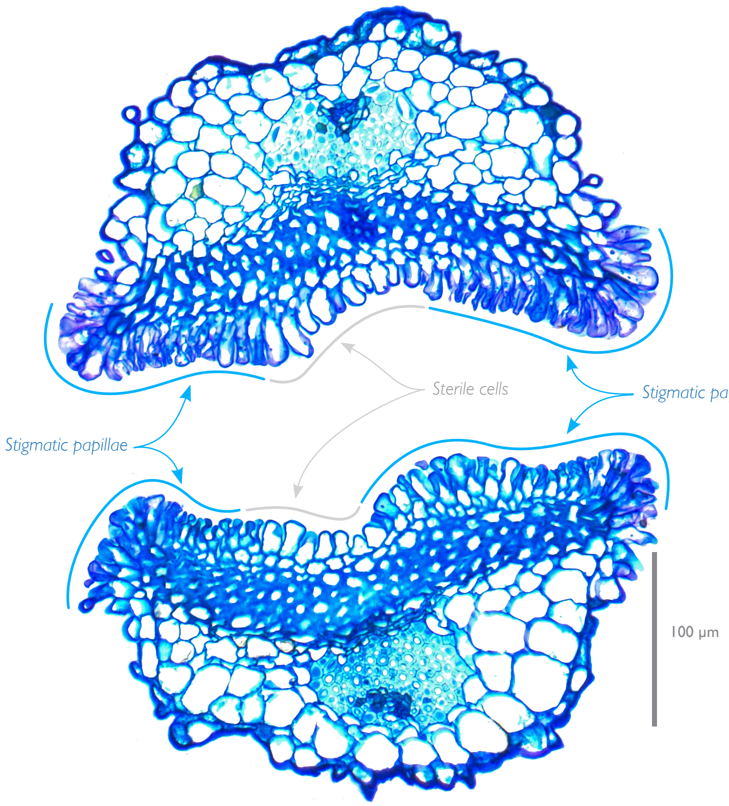


Leucheria suaveolens (Nassauvieae)
Photo by Claudia Erbar & Peter Leins

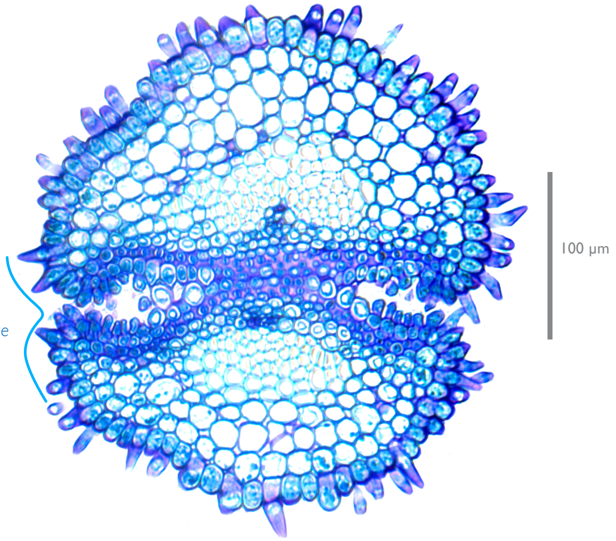
Into the LIGHT

An overlooked feature came to light by histological sections, revealing that stigmatic tissue, in addition to covering the entire inner surface of the style branch or being arranged in two discrete lines, can also take an inversely U-shaped configuration, realized in various ways.

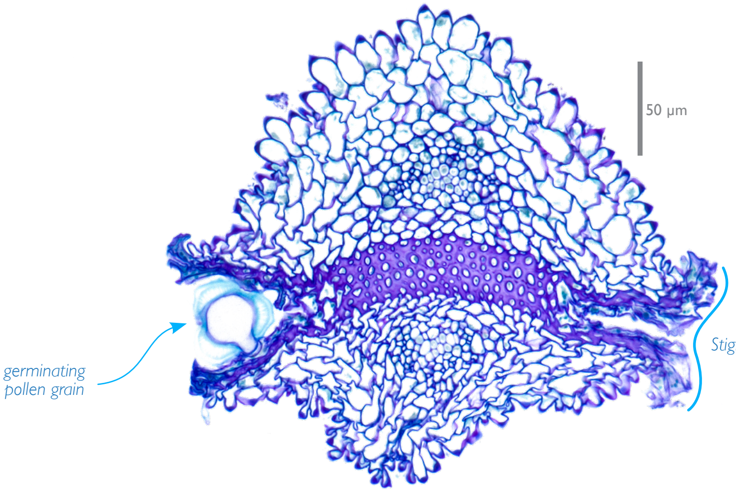
In *Oldenburgia*, two marginal stigmatic bands converge apically. In *Onoseris* and *Carduus*, the U-shaped stigma results from the adhesion of the style branches to each other, facilitated by their median ventral tissues.



Oldenburgia papionum
OLDENBURGIEAE



Carduus defloratus
CARDUEAE



Onoseris odorata
ONOSERIDEAE

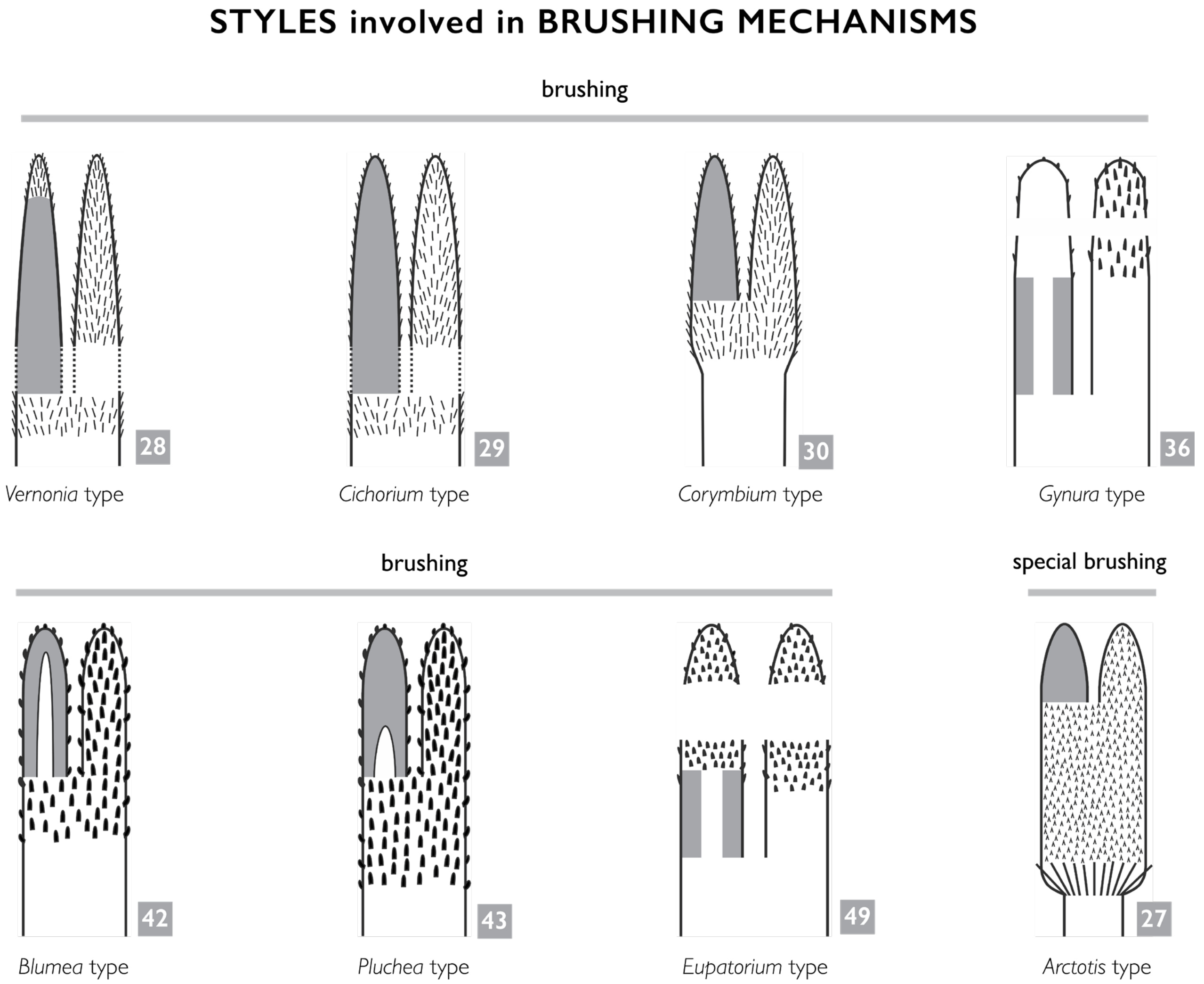


Figure 3. Compilation of style types involved in brushing mechanism The numerals correspond to the style type numbering in Erbar & Leins (2021). Illustrations feature single-plane diagrams rather than perspective drawings. The style branches are rotated 90° and flipped open, allowing both the adaxial (ventral, left) and abaxial (dorsal, right) views to be displayed in the same diagram. Variations in the length of the style branches are only approximated in the illustrations, and additional stylar parts are not depicted. The stigmatic tissue is shaded in grey, and any adhesion zone, if present, is indicated with dotted markings.

In the **brushing mechanism** (Figure 7), the back of the style branches and the upper part of the stylar shaft bear short acute trichomes. In old flower buds, the tip of the style is above the top of the anther tube. Shortly before anthesis, growth of the filaments and the stamen-corolla tube brings the anthers up to the same level as the hairy part of the style so that the style nearly fills the anther tube. The hairy part of the style is as long as the anther tube. The anthers open and the pollen is partly loaded onto the style trichomes. By elongation of the style, the pollen grains are little by little completely swept out of the anthers by the brushing (sweeping) trichomes, which now are somewhat spreading. Thus, once the pollen is released, the hairy part of the style emerges out of the anther tube and gradually presents the pollen on its outside surface (Figure 7B). *Cichorium intybus* L. serves as a representative example of this mechanism, characteristic of the entire tribe Cichorieae.

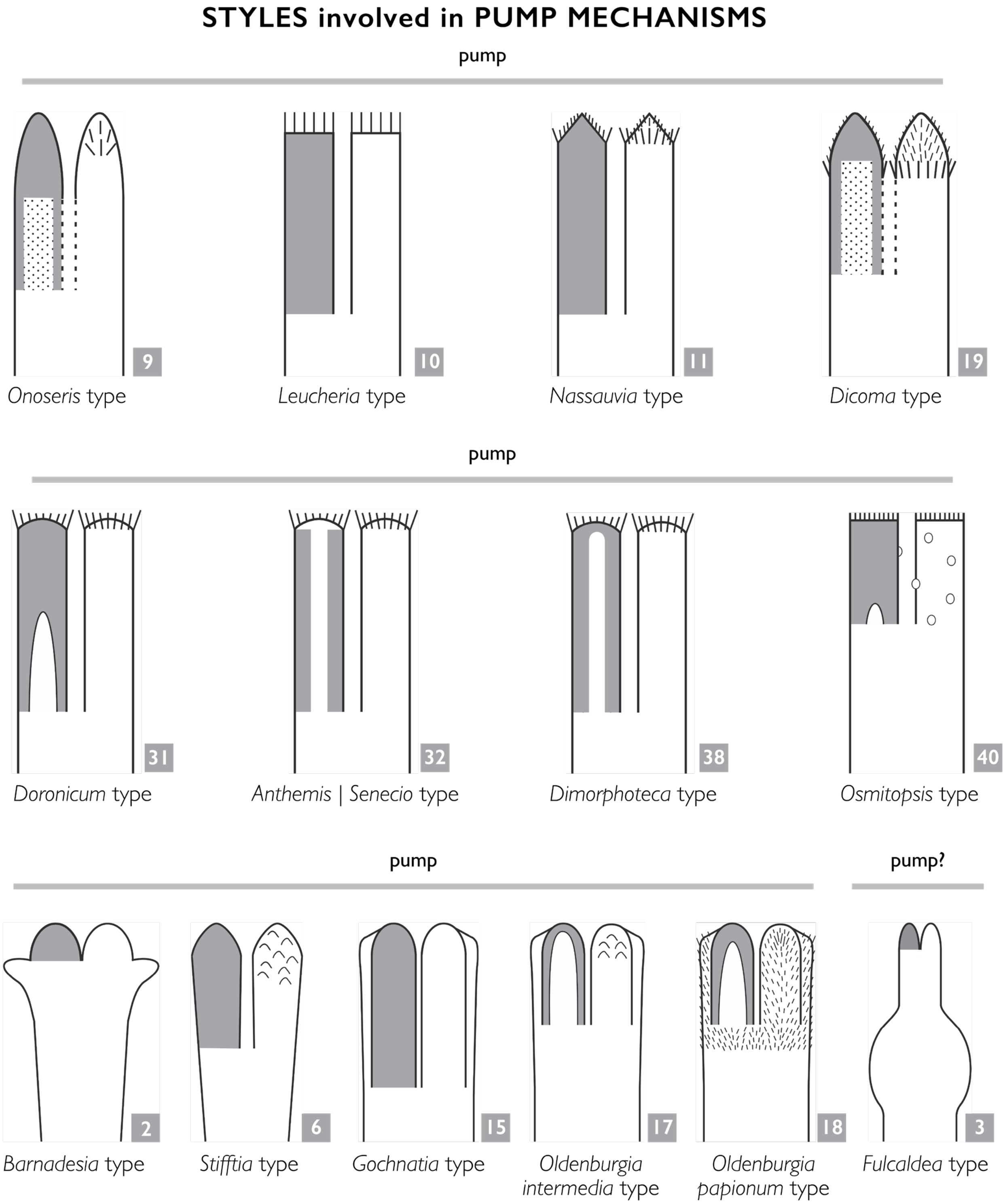


Figure 4. Compilation of style types involved in pump mechanisms. The numerals correspond to the style type numbering in Erbar & Leins (2021). Illustrations feature single-plane diagrams rather than perspective drawings. The style branches are rotated 90° and flipped open, allowing both the adaxial (ventral, left) and abaxial (dorsal, right) views to be displayed in the same diagram. Variations in the length of the style branches are only approximated in the illustrations, and additional stylar parts are not depicted. The stigmatic tissue is shaded in grey, and any adhesion zone, if present, is indicated with dotted markings.

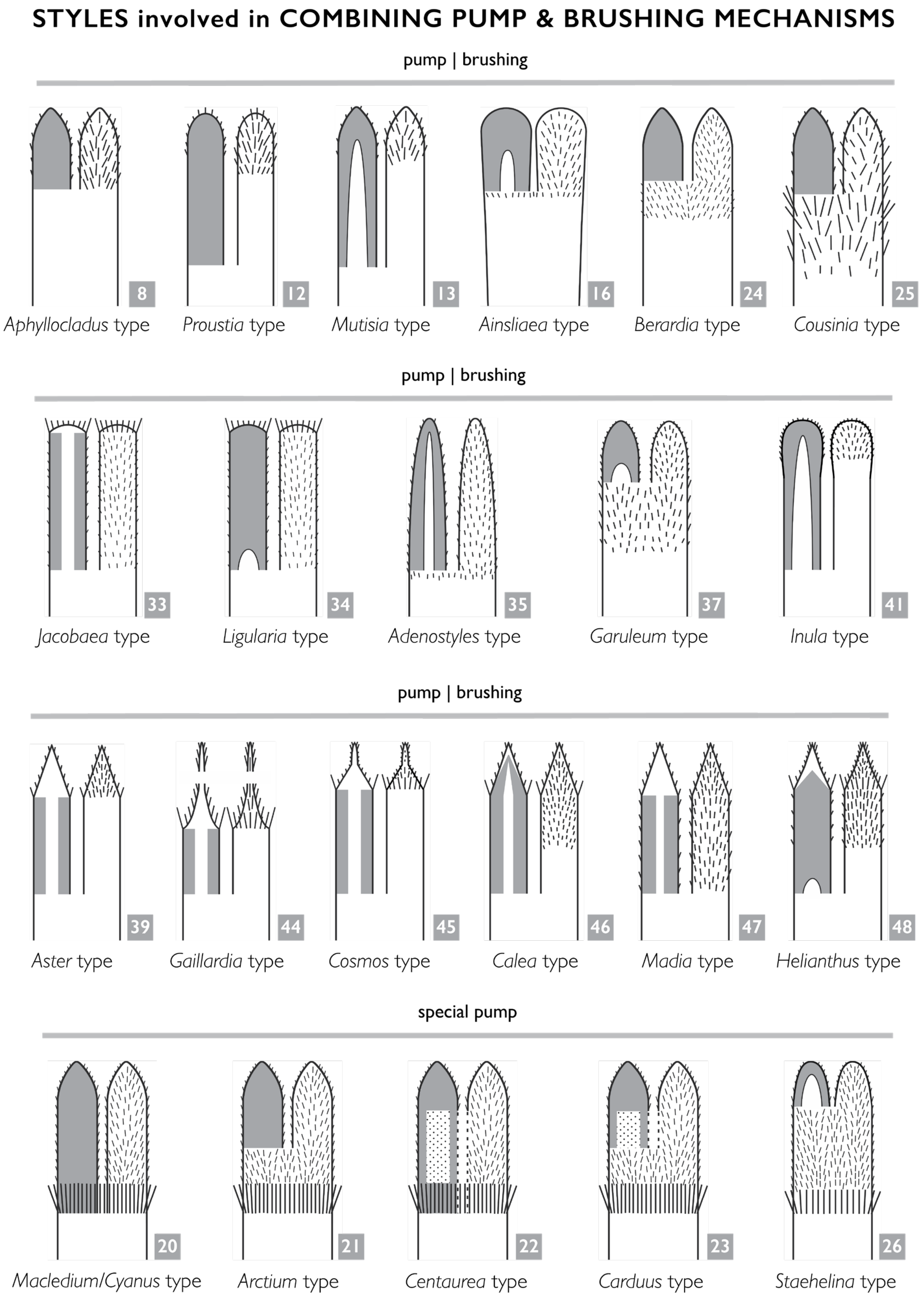


Figure 5. Compilation of style types involved in mechanisms combining pumping and brushing. The numerals correspond to the style type numbering in Erbar & Leins (2021). Illustrations feature single-plane diagrams rather than perspective drawings. The style branches are rotated 90° and flipped open, allowing both the adaxial (ventral, left) and abaxial (dorsal, right) views to be displayed in the same diagram. Variations in the length of the style branches are only approximated in the illustrations, and additional stylar parts are not depicted. The stigmatic tissue is shaded in grey, and any adhesion zone, if present, is indicated with dotted markings.

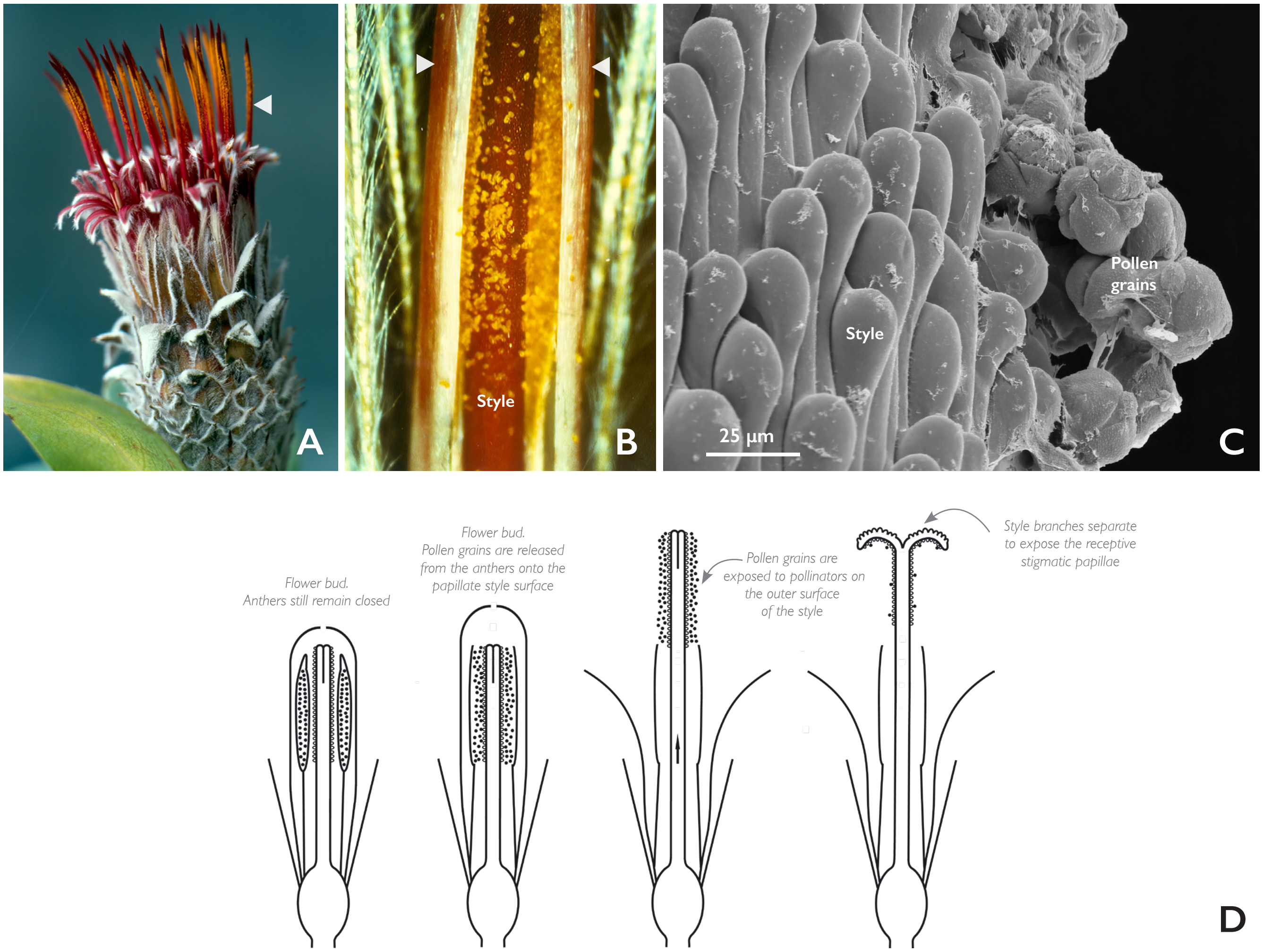


Figure 6. Deposition/simple brushing mechanism, exemplarily shown in *Arnaldoa macbrideana*. **A.** Lateral view of capitulum with styles exposed; arrow indicates pollen grains on outer surface of the style. **B.** Close up of anther tube, indicated with arrows, part of the pollen already deposited onto the style. **C.** SEM image of style with papillate surface and pollen grains attached by abundant pollenkitt. **D.** The deposition/simple brushing mechanism (see Figures 7–13) is illustrated through highly schematic longitudinal sections, adapted from Erbar & Leins (2021). Each sequence, from left to right, depicts different stages, transitioning from a closed flower bud to the exposure of the receptive stigmatic surface at late anthesis.

A pure pump mechanism comes in two variations (Figure 8 and Figure 9). In the **pump mechanism with apical style trichomes** (Figure 8), the style branches mostly are truncate. In older flower buds, the tip of the style is more or less on the same level with the top of the anther tube. Shortly before anthesis, growth of the filaments – supported or even substituted by growth of a stamen-corolla tube – raises the anther tube higher than the stylar tip (Figure 8A). Thus, the tips of the style branches block the lower opening of the anther tube (Figure 8B) and prevent pollen grains falling out when the anthers open and the pollen grains are released into the cavity of the anther tube as a temporary receptacle. After the pollen is released within the anther tube, the elongating style functions as a piston, gradually expelling the pollen from the tube.

Since the connective appendages arch over the anther tube, the pollen exudes from the five slits between them, thus forming a five-pointed star when viewed from above (Figure 8C). As a typical example *Senecio vernalis* Waldst. & Kit. is shown. In general, the **pump mechanism with apical thickening of the style branches** (Figure 9) corresponds to the common pump mechanism (Figure 8). The difference is that the blocking of the lower opening of the anther tube is achieved by apical (or subapical) thickenings of the style branches. Typical examples are *Barnadesia* Mutis ex L.f. species (Figure 9).

In the **special pump mechanism** of Cardueae and Dicomeae (Figure 10), the tip of the style and its proximal collar of trichomes can be found within the anther tube prior to the opening of the anthers. When the corolla opens, growth of stamen-corolla tube and filaments lifts the anther tube to a position in which the style tip remains within the anther tube but the collar of trichomes beneath the hairy stylar part is on the same level as the lower end of the anther tube (Figure 10A). Since the ring of trichomes creates a zone effectively thicker than the distal part of the style, it well blocks the lower opening of the anther tube. The anthers open and the pollen is released into the cavity of the anther tube. The pollen-containing box is extended by considerable apical connective appendages. The growing style then pushes the pollen gradually out (Figure 10B). Pollen grains first protrude from five slits between the connivent anther appendages (Figure 10C) and then pollen heaps are observable above the anther tube's upper end (Figure 10D, yellow arrow). During this early phase of anthesis, small pollen portions

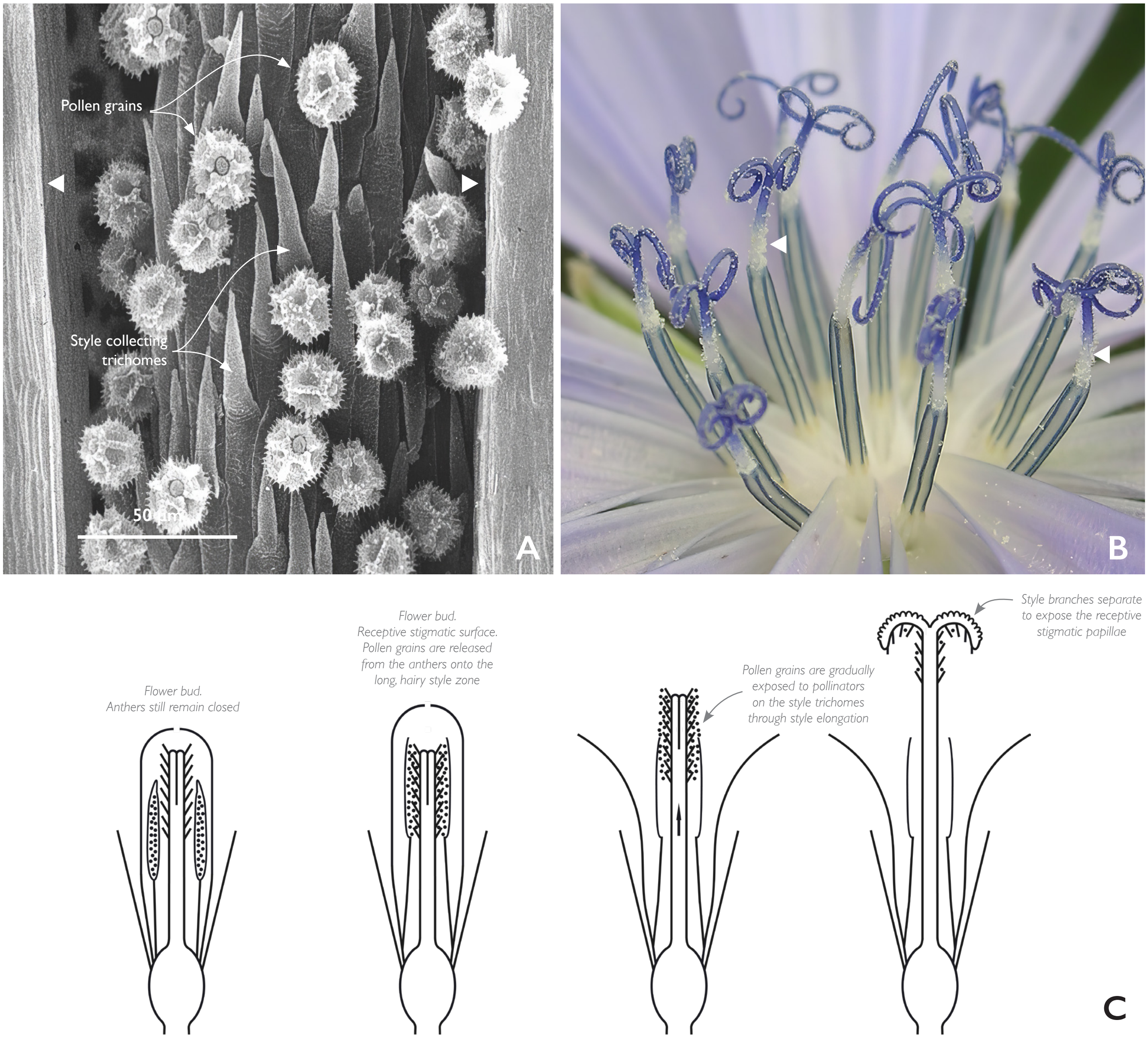
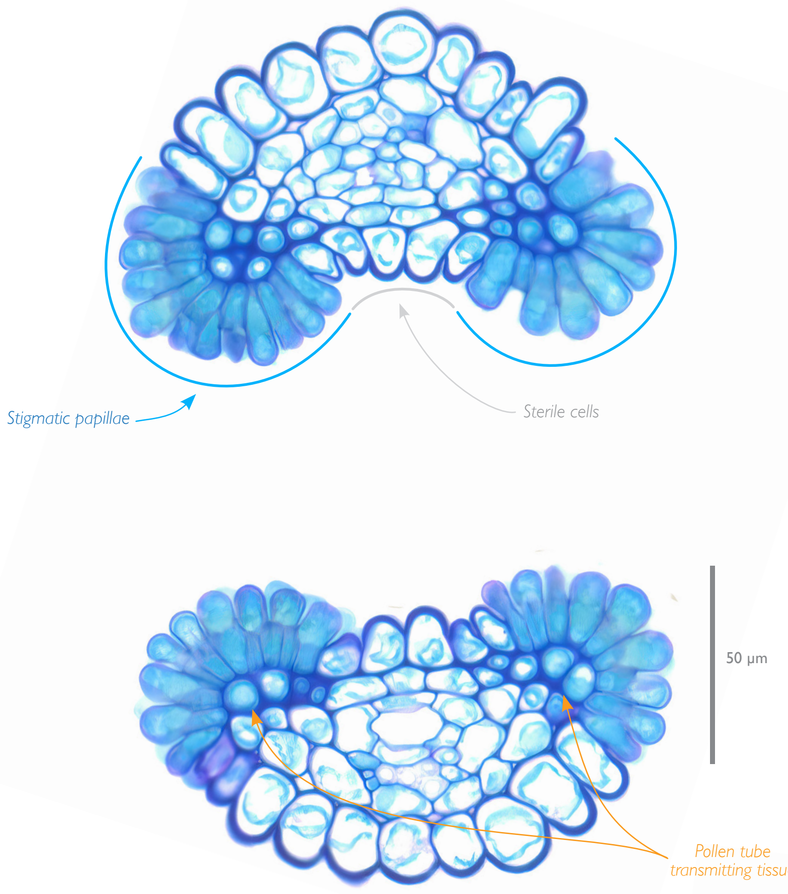


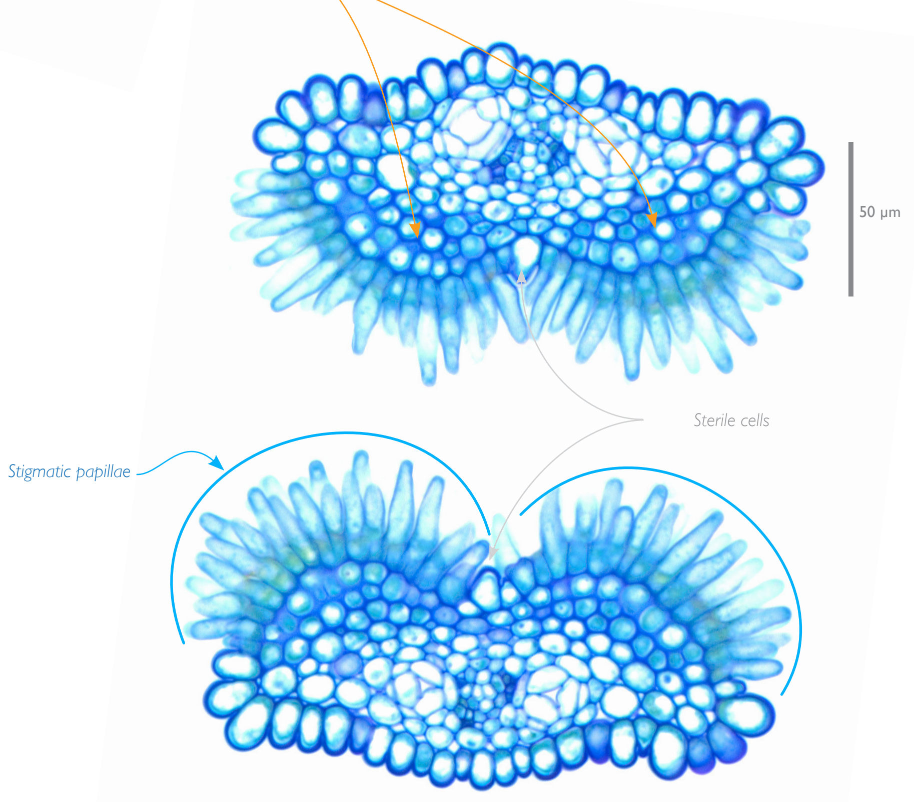
Figure 7. Brushing mechanism, exemplarily shown in *Cichorium intybus*. **A.** SEM image of style shaft still inside anther tube (marked with arrows). **B.** Oblique view of center of capitulum; white arrows indicate pollen grains on style shaft **C.** The brushing mechanism is illustrated through highly schematic longitudinal sections, adapted from Erbar & Leins (2021). Each sequence, from left to right, depicts different stages, transitioning from a closed flower bud to the exposure of the receptive stigmatic surface at late anthesis.

The quintessential stigmatic marginal bands

In most members of the Asteroideae, the stigmatic tissue is organized into two relatively small ventro-marginal bands, as seen in *Anthemis*. However, a recurring trend toward an increased stigmatic surface is evident. For instance, in *Bidens*, the broad stigmatic bands nearly meet but are separated by at least one sterile cell line.



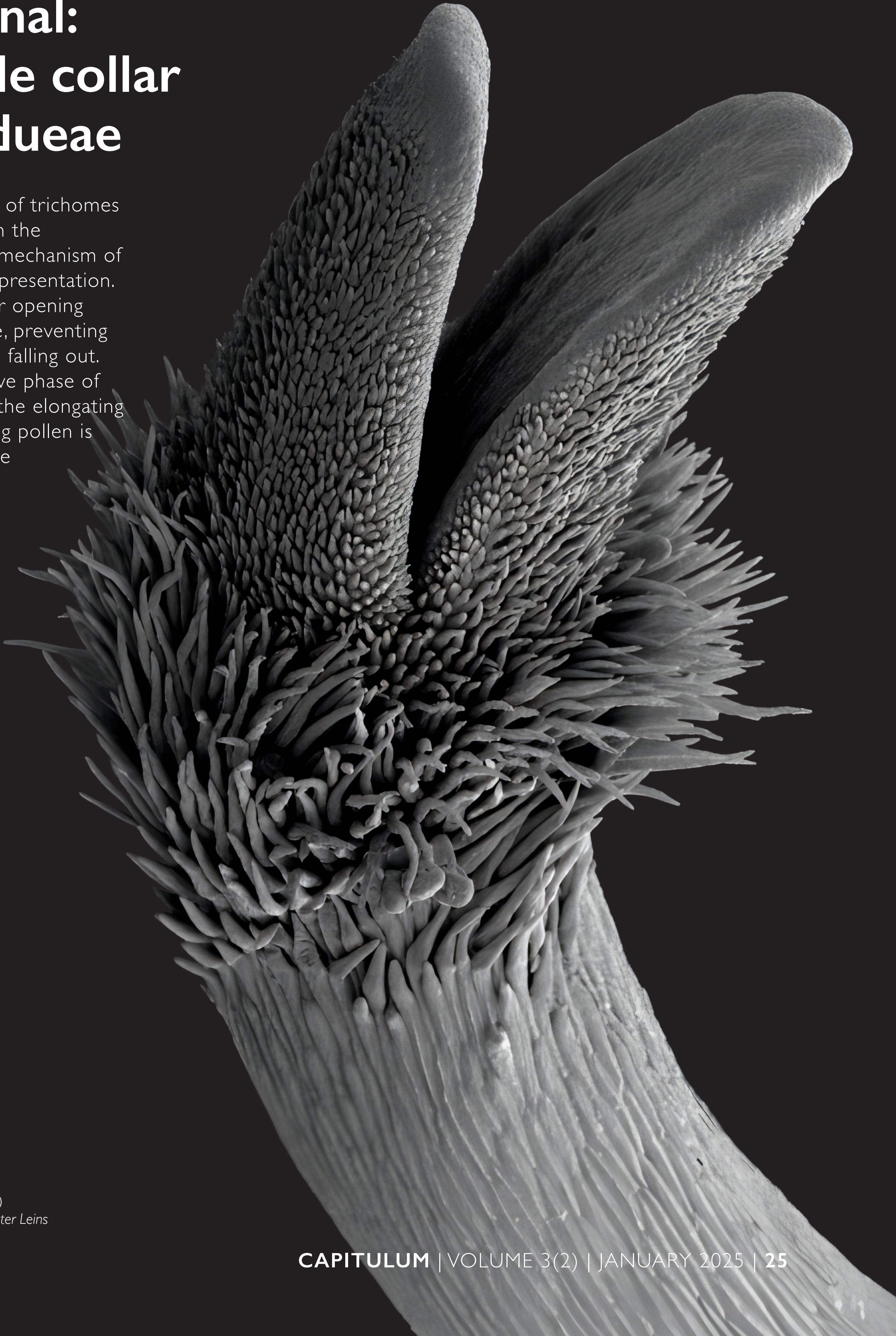
Anthemis maritima
ANTHEMIDEAE



Bidens ferulifolium
COREOPSIDEAE

Showy and functional: the style collar of Cardueae

The distinct collar of trichomes plays a vital role in the specialized pump mechanism of secondary pollen presentation. It blocks the lower opening of the anther tube, preventing pollen grains from falling out. Following the active phase of pollen release by the elongating style, the remaining pollen is brushed out by the collar trichomes.



Cyanus segetum (Cardueae)
Photo by Claudia Erbar & Peter Leins

Flower bud: Anthers still remain closed. The style tip is at the same level as the top of the anther tube

Opening flower. Pollen grains are released into the anther tube, which is raised above the style tip

Pollen grains are gradually exposed to pollinators above the anther tube through style elongation

Style branches separate to expose the receptive stigmatic papillae

Figure 8. Pump mechanism with blocking trichomes, exemplarily shown in *Senecio vernalis*. **A-B.** SEM images show the position of the style with apical trichomes located at the base of the anther tube (indicated by white arrows) during anther opening. **C.** Top view of capitulum; white arrow indicated pollen grains pushed from anther tube through the five slits between the connective appendages. **D.** The pump mechanism is illustrated through highly schematic longitudinal sections, adapted from Erbar & Leins (1995). Each sequence, from left to right, depicts different stages, transitioning from a closed flower bud to the exposure of the receptive stigmatic surface at late anthesis.

are presented. Immediately after, the style emerges from the anther tube with only a moderate or a considerable quantity of pollen on it. To some extent, the short-pilose distal stylar part may act as pollen presenter. The rest of pollen is brushed out by the collar of long trichomes (Figure 10D, white arrow) and pollen grains may be found in this collar even once the stigmatic surface becomes receptive, whereas the distal stylar part is then more or less free of pollen grains. As typical examples *Centaurea nemoralis* Jord. and *Notobasis syriaca* (L.) Cass. are presented.

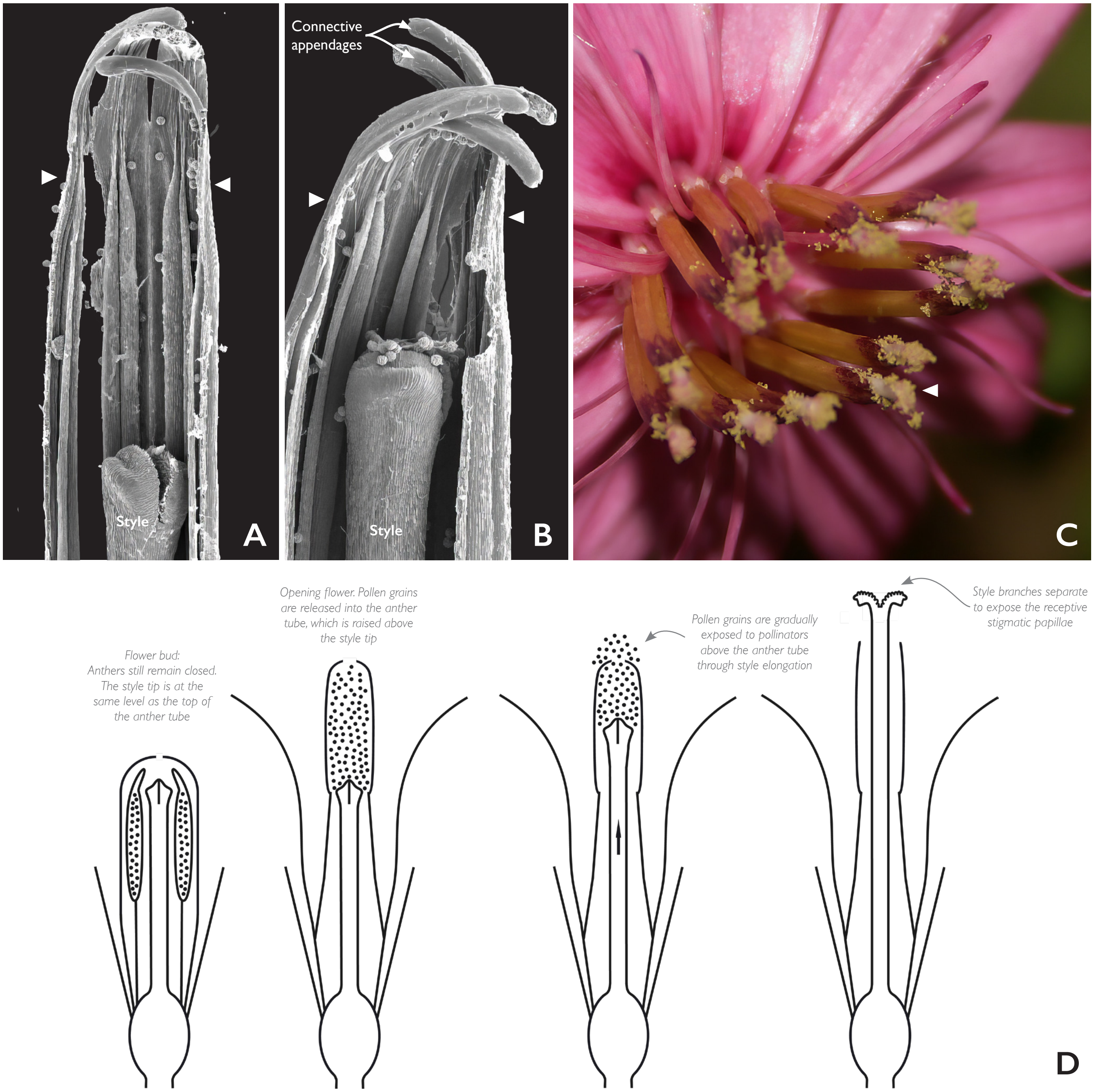
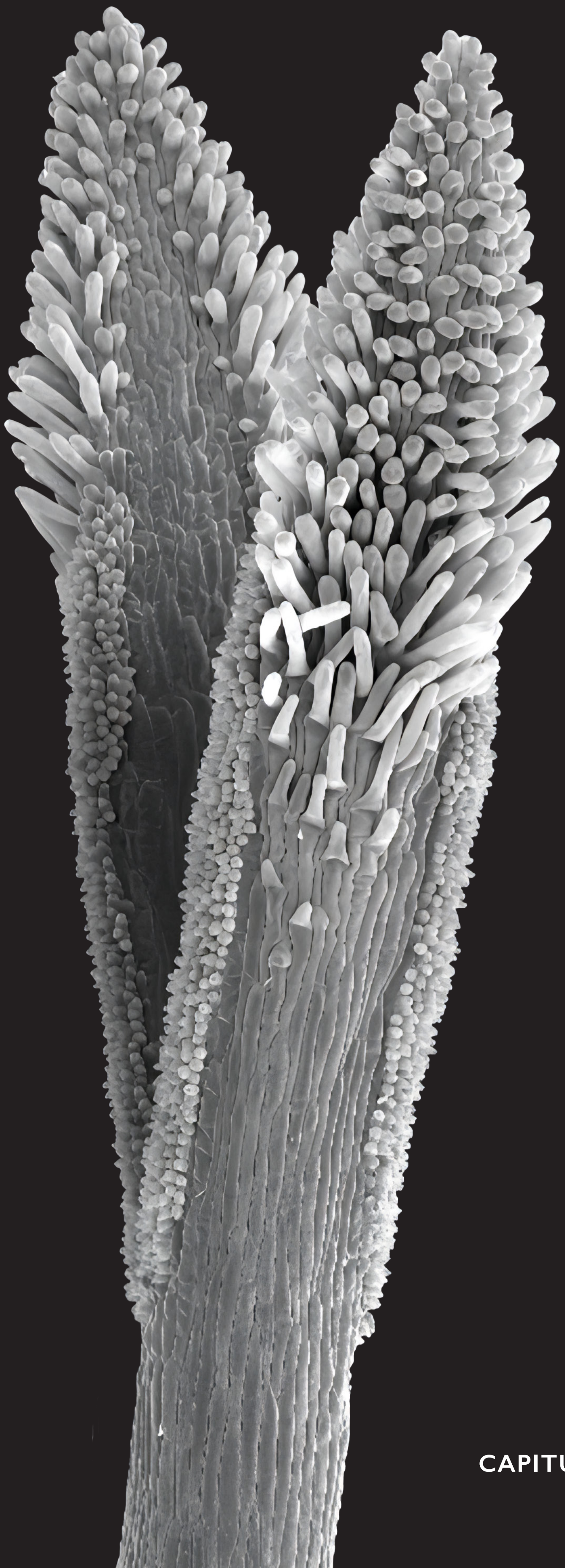


Figure 9. Pump mechanism with apical thickening, exemplarily shown in *Barnadesia*. **A.** SEM image of *B. spinosa* showing the position of the style with apical thickening located at the base of the anther tube; white arrows indicate anther tube. **B.** SEM image of *B. spinosa*, showing the style tip extending close to the upper end of the anther tube; white arrows indicate the anther tube. **C.** Top view of center of capitulum of *B. arborea*; white arrow indicates pollen being pushed out of anther tube. **D.** The pump mechanism is illustrated through highly schematic longitudinal sections, adapted from Erbar & Leins (2021). Each sequence, from left to right, depicts different stages, transitioning from a closed flower bud to the exposure of the receptive stigmatic surface at late anthesis. *Photo credit, image C: D. Brandes, Braunschweig, Germany.*

In the **special brushing mechanism** of Arctotideae and Platycarpheae (Figure 11), the barrel-shaped swelling is proximally delimited by a collar of longer trichomes, distally the barrel and the short style branches are short-pilose. When the anthers open, the upper part of the style, which is abruptly and cylindrically thickened, is equal to the length of the anther tube. The proximal collar of trichomes blocks the lower opening of the anther tube. By growth of the stylar shaft, the barrel-shaped style part emerges



The unmistakable beauty of the Astereae style

The *Aster*-style type is characterized by acute, hairy style branch appendages and clearly separated, discrete lateral stigmatic lines. While this style type is most common in the Astereae, it is also present in the Gnaphalieae, Coreopsideae, Tageteae, and Heliantheae.

Aster alpinus (Astereae)
Photo by Claudia Erbar & Peter Leins

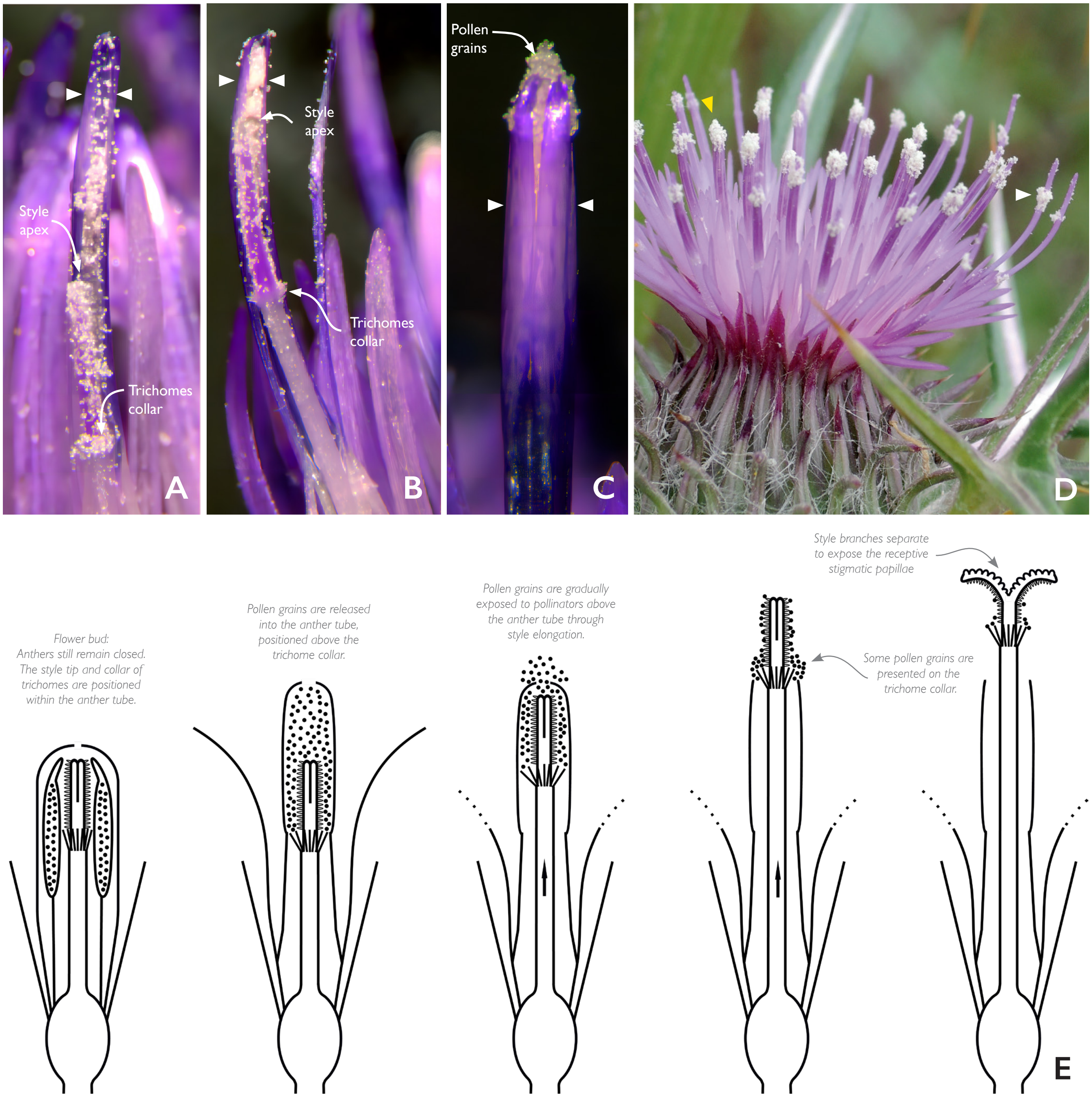


Figure 10. Special pump mechanism. **A–B.** Variations in the position of the style tip and the collar of trichomes within the artificially opened anther tube, caused by style elongation; white arrows indicate anther tube. **C.** Pollen grains emerging between the connivent anther appendages; white arrows indicate anther tube. **D.** Lateral view of capitulum of *Notobasis syriaca;* white arrow indicates collar of trichomes presenting left-over pollen grains; yellow arrow indicates pollen heap at the opening of the anther tube. **E.** The pump mechanism is illustrated through highly schematic longitudinal sections, adapted from Erbar & Leins (2021). Each sequence, from left to right, depicts different stages, transitioning from a closed flower bud to the exposure of the receptive stigmatic surface at late anthesis.

from the anther tube with all the pollen on it (Figure 11A-B), presenting the pollen grains to the visitors (Figure 11C). The mechanism is shown in *Berkheya purpurea* (DC.) Mast.

Several arrangements of style trichomes on the style branches are found in the **combination of pump and brushing mechanism** (Figure 12): long style branches are hairy only in their distal part or

The exclusive and distinctive Asteroideae style

Two distinct ventro-lateral stigmatic bands represent the most common stigma arrangement in the subfamily Asteroideae and are exclusive to it. The *Cosmos*-style type, as shown here, is easily identified by its triangular style branch appendage with a prominently defined tip.

Cosmos bipinnatus (Coreopsideae)
Photo by Claudia Erbar & Peter Leins

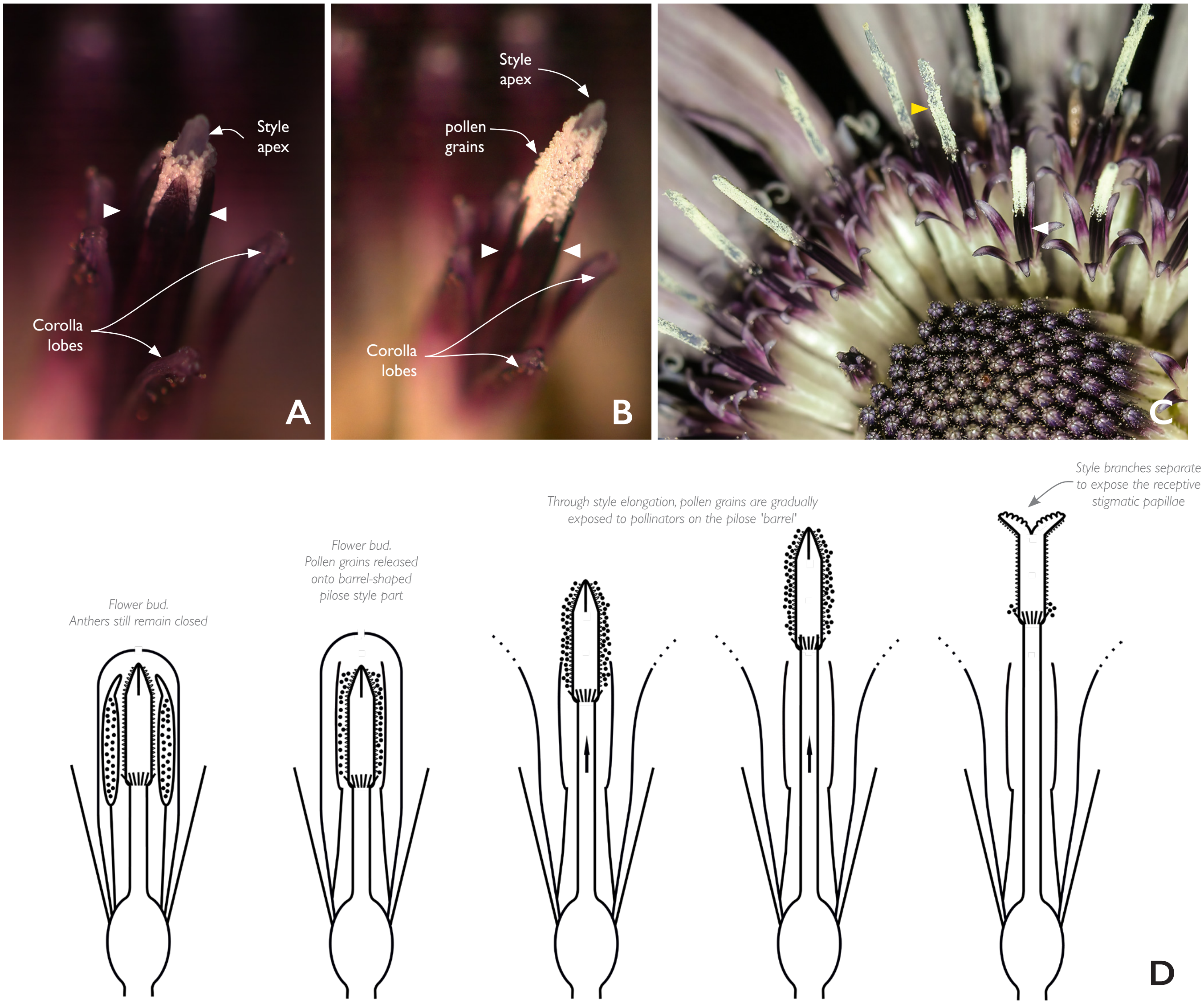


Figure 11. Special brushing mechanism, exemplarily shown in *Berkheya purpurea*. **A-B.** Lateral view of flowers showing the style emerging from the anther tube; white arrows indicate anther tube. **C.** Top view of capitulum; white arrow indicates anther tube, yellow arrow the short-pilose style acting as pollen presenter. **D.** The special brushing mechanism is illustrated through highly schematic longitudinal sections, adapted from Erbar & Leins (2021). Each sequence, from left to right, depicts different stages, transitioning from a closed flower bud to the exposure of the receptive stigmatic surface at late anthesis.

rather short style branches are hairy over their entire length (and even beneath the bifurcation). In the case of short style branches, these are shorter than the anther tube. In the case of truncate style branches, a tuft of trichomes is present (sub) apically, with shorter trichomes extending dorsally along a portion of the stylar branch length. At anther dehiscence, the position of the stylar tips is correlated with the distribution of style trichomes. It is only the hairy part of the style that is embedded within the anther tube (Figure 12A). Some pollen is shed into the anther tube, some onto the stylar hair zone. Thus, by style elongation, some pollen is pushed out, and some is brushed out. At first, in the pumping phase, the pollen exudes from the slits between the connective appendages (note the "five-pointed star" when viewed from above, Figure 12B). Later on, the hairy part of the style emerges out of the anther tube and presents the pollen on its outside (Figure 12C). As examples *Bellis annua* L. and *Galatella linosyris* (L.) Rchb.f. in the Astereae tribe are chosen. A variation is the last mechanism, a **combination of pump and slightly brushing mechanism with apical pollen presentation** (Figure 13), in which the style branches possess long sterile appendages. These are triangular or

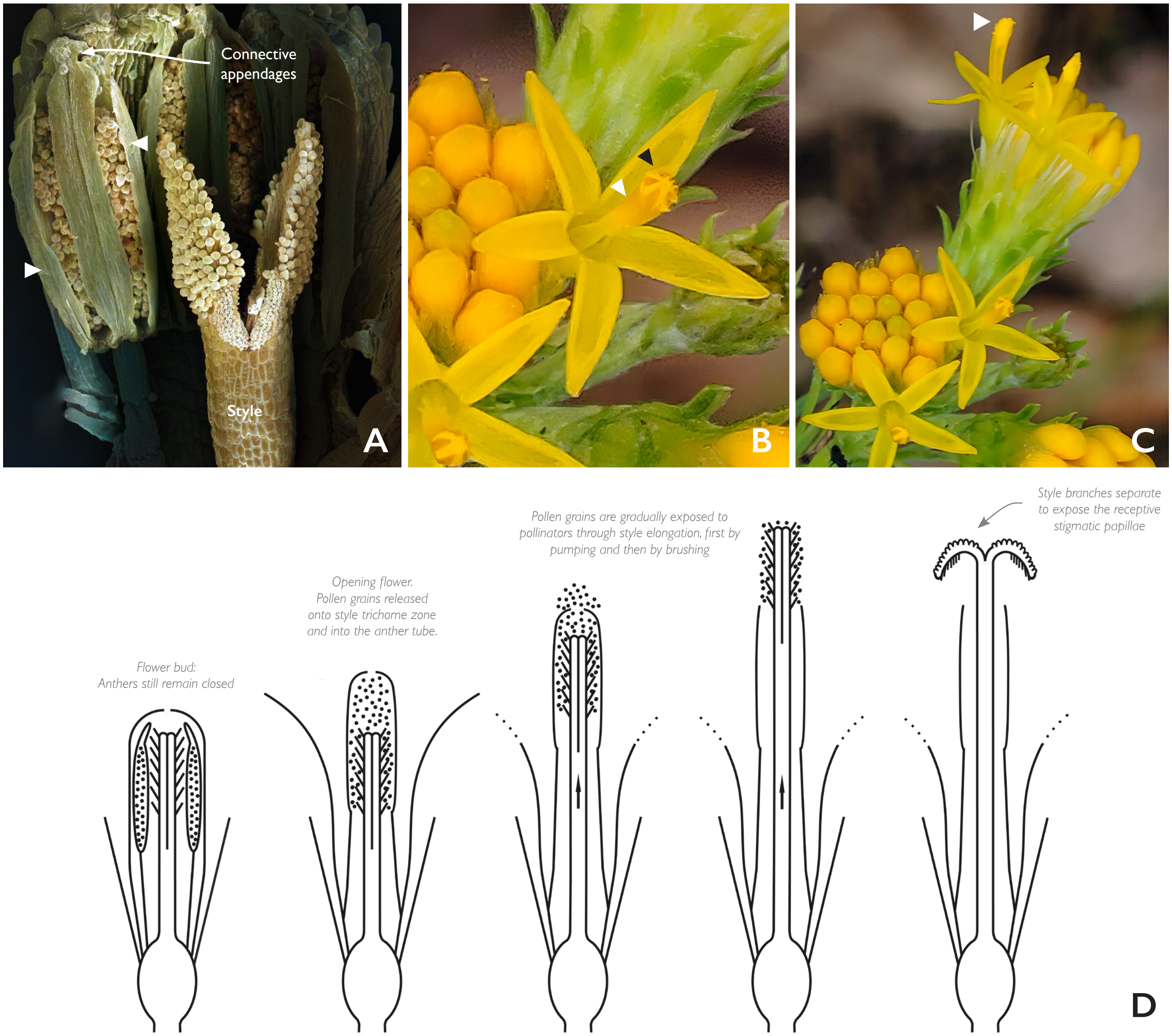


Figure 12. Combination of pump and brushing mechanism. **A.** SEM image showing a lateral view of a monoclinous disc flower of Bellis annua (artificially opened). At the time of anther dehiscence, only the hairy portion of the style remains embedded within the anther tube (indicated by white arrows). **B.** Top view of flower of *Galatella linosyris*; white arrow indicates anther tube; black arrow point to pollen grains protruding from five slits between the connivent anther appendages (pumping phase). **C.** Lateral view of capitulum of *Galatella linosyris*; white arrows indicate brushed-out pollen grains located on the outer surface of the style branches. **D**. The combination of pump and brushing mechanism is illustrated through highly schematic longitudinal sections, adapted from Erbar & Leins (2021). Each sequence, from left to right, depicts different stages, transitioning from a closed flower bud to the exposure of the receptive stigmatic surface at late anthesis.

narrow and long or tapering or even with a markedly defined tip. At anther dehiscence, the hairy area of the style branches or some longer style trichomes at the base of the appendages block the lower opening of the anther tube (Figure 13A). Pollen is shed into the anther tube, in the middle of which to a small or (mostly) large extent the stylar appendages are located. The growing style pushes some pollen out (Figure 13B), the remaining pollen grains are hold by the stylar appendages during the style elongation and the pollen presenting phase of anthesis (Figure 13C). The mechanism is exemplarily shown in *Bidens ferulifolia* (Jacq.) Sweet (Coreopsideae).

In a simplistic and comprehensive way, we can further subsume these eight mechanisms into four main functional categories: deposition, brushing,

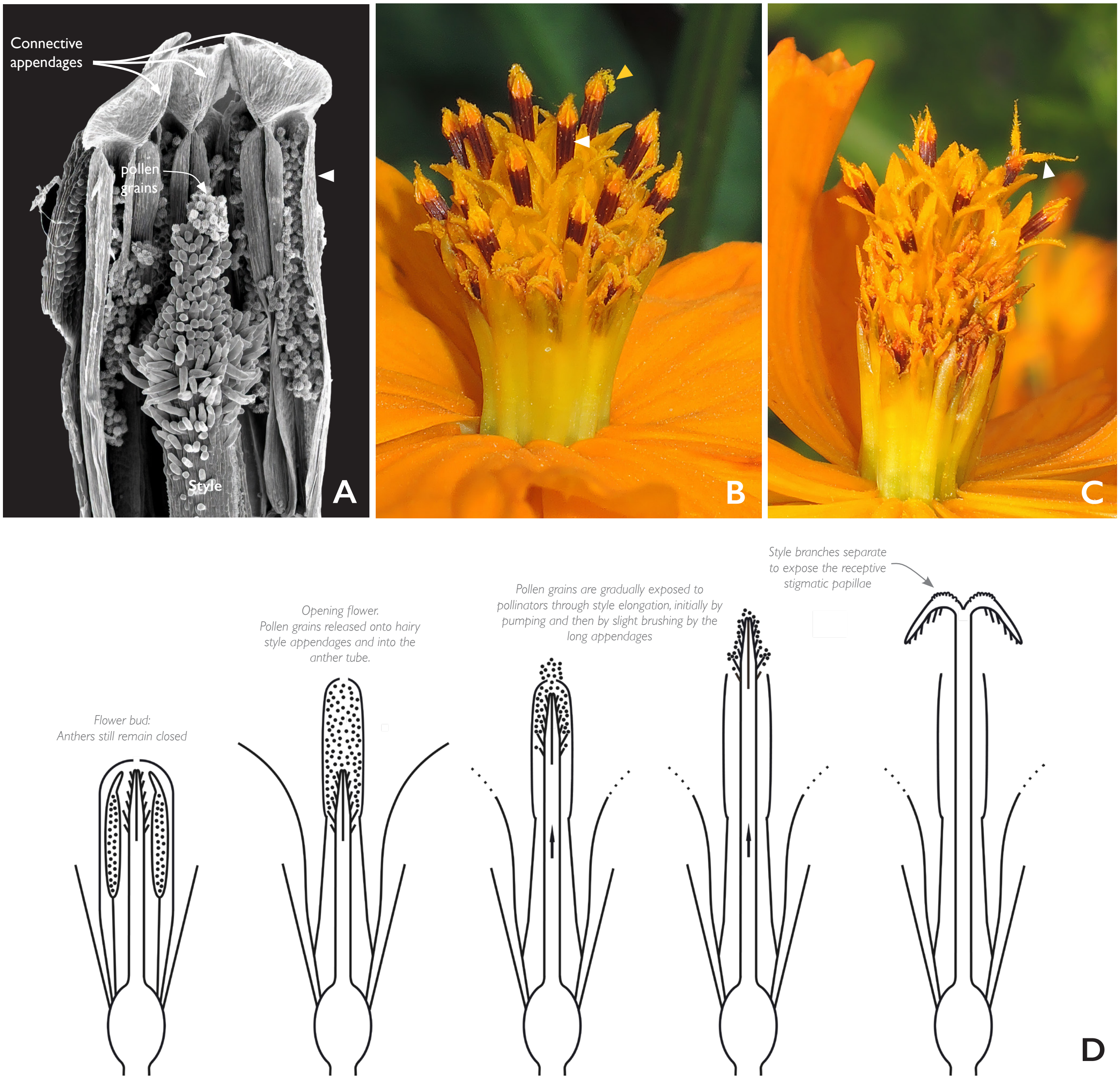
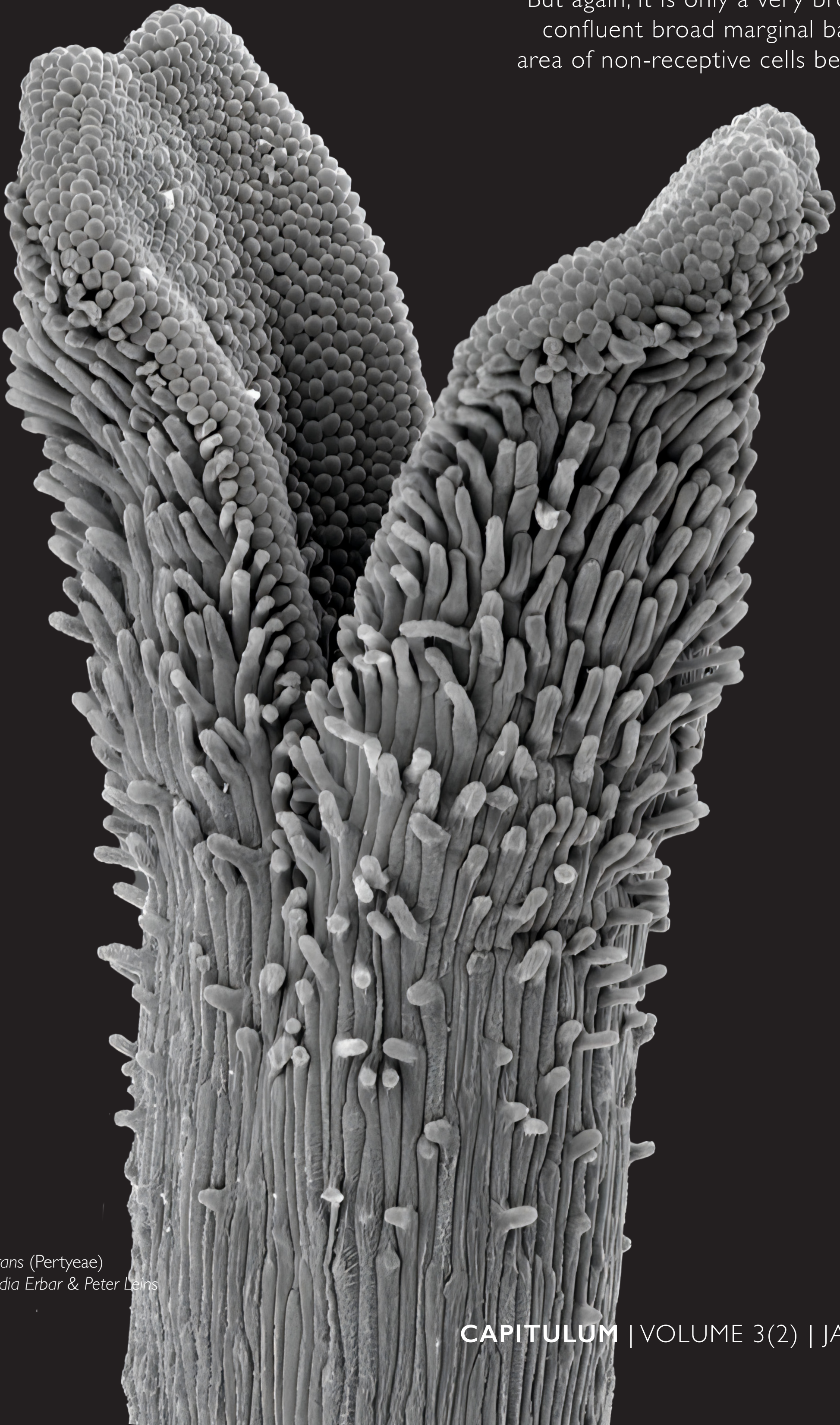


Figure 13. Combination of pump and slightly brushing mechanism with apical pollen presentation, exemplarily shown in *Bidens ferulifolium*. **A.** SEM image of the anther tube (indicated by a white arrow), showing the style with long appendages beginning to elongate shortly after anther opening. **B.** Lateral view of center of capitulum; white arrow indicates anther tube; yellow arrow points to pollen grains protruding from five slits between the connivent anther appendages. **C.** Lateral view of capitulum; white arrows mark pollen grains at the outside of the style branches. **D**. The combination of pump and slightly brushing mechanism is illustrated through highly schematic longitudinal sections, adapted from Erbar & Leins (2021). Each sequence, from left to right, depicts different stages, transitioning from a closed flower bud to the exposure of the receptive stigmatic surface at late anthesis.

pump, and pump and brushing combined. These simplifications allow for easier comparison when plotting the different mechanisms onto a phylogenetic tree (Figure 14). Five style types are involved in deposition mechanisms (Figure 2). These types as well as the mechanisms are confined to basal groups of Asteraceae (Figure 14). The rounded flat papillae or scale-like bi- to tri-seriate style trichomes in these styles are not suitable for efficient sweeping, but nevertheless contribute to

The great pretender

Superficially, stigmatic tissue appears to cover the entire inner surface of the style branches. But again, it is only a very broad zone of apically confluent broad marginal bands, leaving a small area of non-receptive cells between them basally.



Ainsliaea fragrans (Pertyeae)
Photo by Claudia Erbar & Peter Leins

some brushing in the secondary pollen presentation. In contrast, acute style trichomes characterize the pure brushing mechanism (three style types, #28–30 in Figure 3), which is the only mechanism in Cichorieae, Corymbieae, Eremothamneae, Liabeae, Moquinieae, and Vernonieae (Figure 14). In the special brushing mechanism of Arctotideae and Platycarpheae also acute style trichomes are present (#27 in Figure 3). Outside the Vernonioideae-Cichorioideae-Corymbioideae relationship, a pollen brushing accomplished by acute style trichomes is not found. The other four style types involved in pollen brushing (#36, 42, 43, 49; Figure 3) are characterized by obtuse or rounded style trichomes (in *Gynura* [Senecioneae], Inuleae, Athroismeae, Tageteae, and Eupatorieae). Pure pump mechanisms need styles that efficiently block the lower end of the anther tube (Figure 4). The blocking is achieved either by more or less prominent dorsal thickenings or by transverse bulges, apically dilating the style branches (Figure 4, lower row). Truncate or more or less rounded style branches with style trichomes only at the very tips of the style branches (mostly an apical, seldom a subapical tuft of style trichomes) characterize eight further style types (Figure 4, upper and middle rows). Pump mechanisms are found across the whole family (Figure 14).

A large number of style types (22 of 49) is involved in a combination of pump and brushing mechanisms (Figure 5). In general, we can predict the relative involvement of pumping and brushing, respectively, from the relative length of the hairy zone of the style. The special pump mechanism – confined to members of Carduoideae (Dicomeae and Cardueae) and realized by five style types that are characterized by a ring of trichomes beneath a hairy stylar part (Figure 5, lower row) – is essentially a pump mechanism (and treated as such in Figure 14). However, to some extent, the short-pilose distal stylar part acts as pollen presenter and pollen grains are brushed out by a collar of long trichomes, so that we arranged the corresponding style types in this comparative consideration in Figure 5.

It has to be mentioned that in staminate flowers with sterile styles, pure brushing and pure pump mechanisms as well as combinations of pump and brushing mechanisms occur (Figure 14).

FINAL REMARKS

Modern sequence analysis has become more and more established in recent years and the detailed and refined analyses provide a basis for the present classifications of Asteraceae. Nevertheless, style morphology and anatomy seems to be meaningful as well as in systematic and taxonomic considerations on a higher level. Furthermore, the style of the Asteraceae, seems in terms of its biological relevance, i.e., its functionality, to be an efficient concept for success, due to which the family owes its immense diversity of species. Along with other special flower structures (stamen-corolla tube, anther tube) and their growth behaviour, the style serves as a successful pollen presenter in the mechanisms of pollen portioning. As a rule, the mechanisms of secondary pollen presentation ensure a gradual delivery of small pollen portions to pollinators over time. Generally speaking, the size of the pollen portion is correlated with many other parameters of flower functions (see the multifactorial net of correlations concerning flower functions; Fig. 164 in Leins & Erbar, 2010). The delivery of numerous small pollen portions, the dense inflorescences (capitula), the reduction to a single ovule per flower, the long time of pollen presentation during anthesis at the level of each flower, capitulum, and individual plant (often bearing multiple capitula), as well as the open structure of the pseudanthium, which allows pollinators to move freely, collectively contribute to the ecological generalization of most Asteraceae. This generalist strategy, in terms of flower and pollination ecology, is further supported by the high number of pollen application sites available to pollinators. They have a large spectrum of different pollinators such as beetles, bees, wasps, flies and butterflies. This can lead to a considerable loss of pollen, since some of these flower-visiting insects may be unreliable concerning the repeated visit of the same plant species. Nevertheless, loss of pollen through "vagabonds" can be reduced by limiting the amount of pollen offered by a flower at a time by the mechanisms of secondary pollen presentation (pollen portioning; see, e.g., Leins & Erbar, 2006, 2010).

Secondary pollen presentation is also found among Asteraceae closest relatives in the Asterales. The sister family Calyceraceae exhibits a pure, simple deposition mechanism (Erbar, 1993): The pollen grains

SECONDARY POLLEN PRESENTATION
Across COMPOSITAE

- 🟨 Brushing
- 🟩 Pump
- 🟩 Combined Pump & Brushing
- 🟦 Deposition/Brushing
- ☐ Staminate flowers

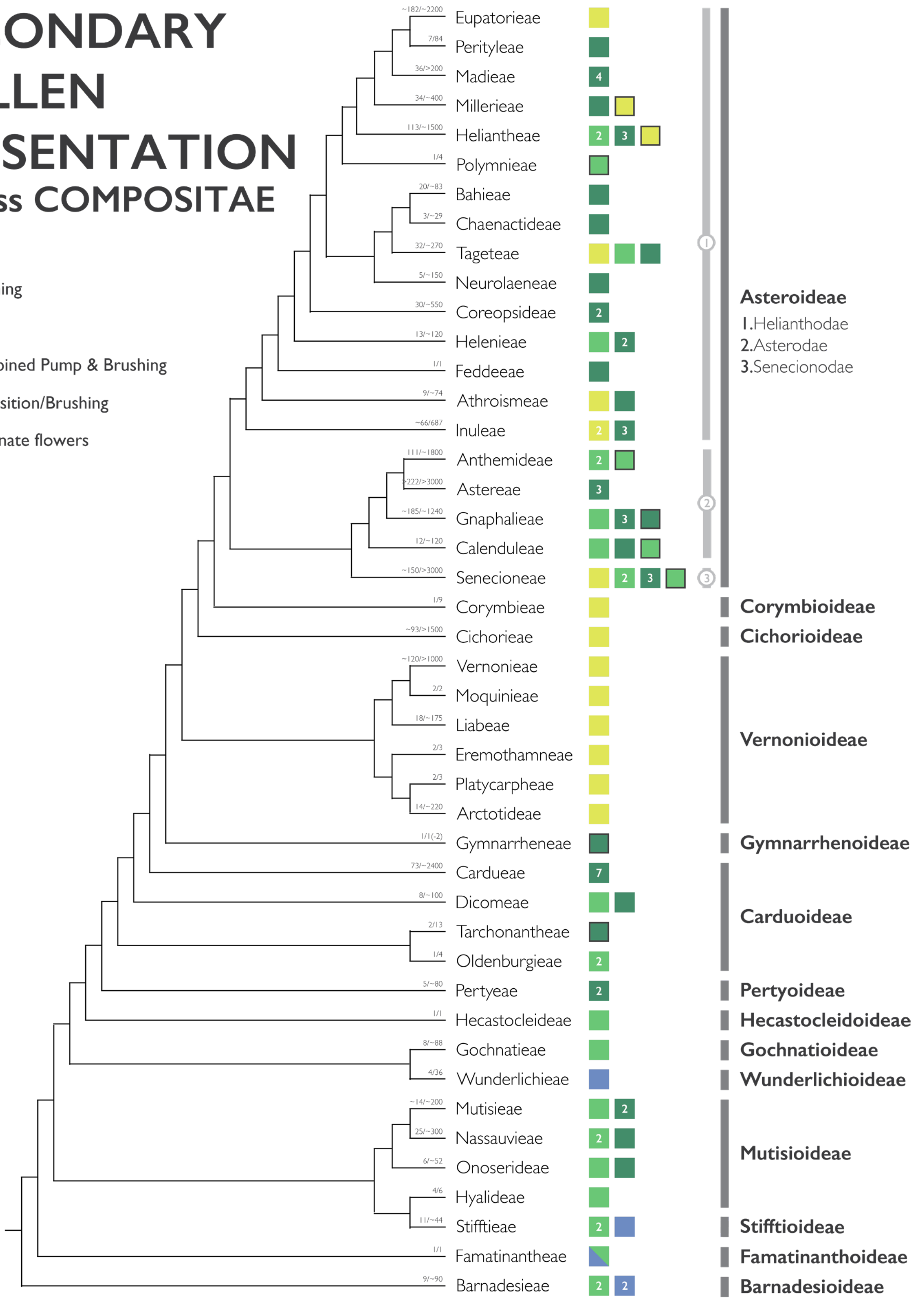


Figure 14. Generalized phylogenetic tree of Asteraceae (based on Funk et al., 2009b; Panero et al., 2014; Mandel et al., 2019) onto which the different mechanisms of secondary pollen presentation are plotted. The numerals inside boxes indicate number of style types exhibiting the corresponding mechanism. As regards closely related families, Calyceraceae exhibit a pure deposition mechanism, and Goodeniaceae a cup mechanism (confined to this family).

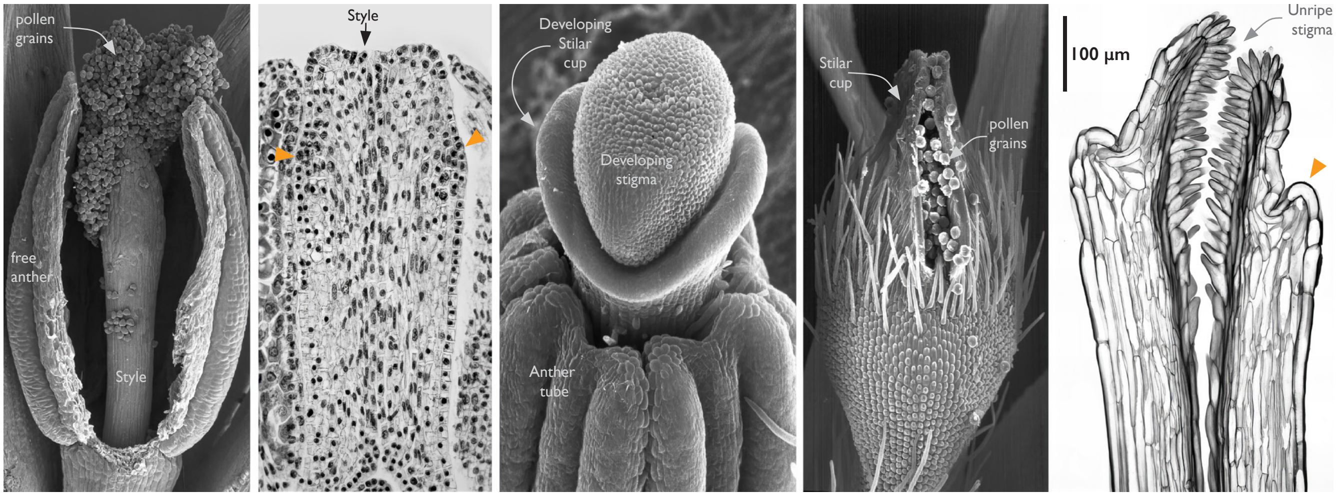


Figure 15. A. Simple deposition mechanism of secondary pollen presentation in *Acicarpha tribuloides* (Calyceraceae). B-D. *Brunonia australis* (Goodeniaceae). **B-C.** Early development of the stylar cup as outgrowth by cell divisions (orange arrows in B) beneath the stylar tip. **D.** Own pollen grains within the stylar cup before presented to pollinators by growth of the developing stigma. **E.** *Barnadesia polyacantha* (Asteraceae-Barnadesieae). The transverse bulges, typical of the *Barnadesia*-style type, correspond to the cup in Goodeniaceae in the position, but are formed by very late elongation of cells beneath the epidermis (orange arrow).

are deposited onto the style and the style emerging from the anther tube gradually presents the pollen on its outside. It merely requires a spreading of the emptied anthers for an unimpeded presentation of the pollen by lengthening of the style (Figure 15A; Erbar, 1993; Leins & Erbar, 2010). We assume that this mechanism is transferred as the first one to the basal Asteraceae. Nowadays Goodeniaceae are regarded as sister to Calyceraceae and Asteraceae. The cup mechanism of Goodeniaceae, confined to this family, is a specialized deposition mechanism (Erbar & Leins, 1988; Leins & Erbar, 2010). The cup-like structure beneath the tip of the style takes up the whole pollen mass (Figure 15D); later, the developing stigma gradually pushes out the pollen. The position of stylar cup and the bulges in *Barnadesia* are comparable, but there is a crucial difference in the ontogeny of both stylar structures. The stylar cup in Goodeniaceae is a very early outgrowth by cell divisions beneath the stylar tip Figure 15B-C; Erbar & Leins, 1988; Leins & Erbar, 1989), whereas in *Barnadesia*, the bulges are formed very late by elongation of cells beneath the epidermis (Figure 15E).

In conclusion, apart from the high diversity of style types within the Asteraceae, the specific and economical delivery of pollen grains onto pollinators through the mechanisms of secondary pollen presentation may be one of the key factors underlying the great evolutionary success of the family, in terms of species richness and distribution in diverse habitats almost anywhere in the world.

ACKNOWLEDGEMENTS

We express our heartfelt gratitude to Mauricio Bonifacino for suggesting the idea of summarizing our detailed research into an article for ***Capitulum***. We extend special thanks to him for the outstanding presentation and meticulous compilation of our SEM images of the styles. Additionally, we are deeply grateful to the reviewers and, in particular, to the editors for their insightful and valuable suggestions.

LITERATURE CITED

Bentham, G. 1873. Notes on the classification, history, and geographical distribution of Compositae. *J. Linn. Soc.* 13: 335–577.

Berkhey, J. Le Francq van 1760. Expositio Characteristica Structurae Florum qui Dicuntur Compositi. Leiden: Van der Eyk.

Bremer, K. 1987. Tribal interrelationships of the Asteraceae. *Cladistics* 3(3): 210–253.

Bremer, K. 1994. Asteraceae: Cladistics and Classification. Portland: Timber Press.

Cassini, H. 1826. Opuscules Phytologiques, vols. 1–2. – Paris: Levrault.

Erbar, C. 1993. Studies on the floral development and pollen presentation in *Acicarpha tribuloides* with a discussion of the systematic position of the family Calyceraceae. *Bot. Jahrb. Syst.* 115: 325–350.

Erbar, C. & Leins, P. 1988. Studien zur Blütenentwicklung und Pollenpräsentation bei *Brunonia australis* Smith (Brunoniaceae). *Bot. Jahrb. Syst.* 110: 263–282.

Erbar, C. & Leins, P. 2015. Diversity of styles and mechanisms of secondary pollen presentation in basal Compositae – new insights in phylogeny and function. *Flora* 217: 109–130.

Erbar, C. & Leins, P. 2016. Styles and new stigma characters in Mutisieae s.str. (Asteraceae-Mutisioideae) in comparison with genera of traditionally circumscribed Mutisieae. *Plant Div. Evol.* 131: 363–393.

Erbar, C. & Leins, P. 2021. Style diversity in Asteraceae: morphology, anatomy, phylogeny, and function. *Bibliotheca Botanica* 163: 1–260.

Funk, V.A., Susanna, A., Stuessy, T.F. & Bayer, R.J. 2009a. Systematics, Evolution, and Biogeography of Compositae. Vienna: IAPT.

Funk, V.A., Anderberg, A.A., Baldwin, B.G., Bayer, R.J., Bonifacino, M., Breitwieser, I., Brouillet, L., Carbajal, R., Chan, R., Coutinho, A.X.P., Crawford, D.J., Crisci, J.V., Dillon, M.O., Freire, S.E., Galbany-Casals, M., Garcia-Jacas, N., Gemeinholzer, B., Gruenstaeudl, M., Hansen, H.V., Himmelreich, S., Kadereit, J.W., Källersjö, M., Karaman-Castro, V., Karis, P.O., Katinas, L., Keeley, S., Kilian, N., Kimball, R.T., Lowrey, T.K., Lundberg, J., McKenzie, R.J., Tadesse, M., Mort, M.E., Nordenstam, B., Oberprieler, C., Ortiz, S., Pelser, P.B., Randle, C.P., Robinson, H., Roque, N., Sancho, G., Semple, J.C., Serrano, M., Stuessy, T.F., Susanna, A., Unwin, M., Urbatsch, L., Urtubey, E., Vallès, J., Vogt, R., Wagstaff, S., Ward, J., Watson, L.E. 2009b. Compositae metatrees: The next generation. – In: Funk, V.A., Susanna, A., Stuessy, T.F. & Bayer, R.J. (eds.), Systematics, Evolution, and Biogeography of Compositae. 747–777. Vienna: IAPT.

Heywood, V.H., Harborne, J.B. & Turner, B.L. 1977. Biology and Chemistry of the Compositae. London: Academic Press.

Hildebrand, F. 1870. Ueber die Geschlechtsverhältnisse bei den Compositen. *Nov. Act. Acad. Caes. Leop.-Carol.* 35: 1–104 + 6 plates.

Hoffmann, O. 1894. Compositae. In: Engler, A., Prantl, K. (eds.), Die natürlichen Pflanzenfamilien IV.5: 87–387. – Leipzig: Engelmann.

Leins, P. & Erbar, C. 1989. Zur Blütenentwicklung und sekundären Pollenpräsentation bei *Selliera radicans* Cav. (Goodeniaceae). *Flora* 182: 43–56.

Leins, P. & Erbar, C. 1990. On the mechanisms of secondary pollen presentation in the Campanulales-Asterales-complex. *Botanica Acta* 103: 87–92.

Leins, P. & Erbar, C. 2006. Secondary pollen presentation syndromes of the Asterales – a phylogenetic perspective. *Bot. Jahrb. Syst.* 127: 83–103.

Leins, P. & Erbar, C. 2010. Flower and Fruit. Morphology, Ontogeny, Phylogeny, Function and Ecology. Stuttgart: Schweizerbart Science Publishers.

Lessing, C.F. 1832 Synopsis Generum Compositarum, earumque dispositionis novae tentamen, monographiis multarum Capensium interjectis. Berlin: Duncker & Humblot.

Mandel, J.R., Dikow, R.B., Siniscalchi, C.M., Thapa, R., Watson, L.E. & Funk, V.A. 2019. A fully resolved backbone phylogeny reveals numerous dispersals and explosive diversifications throughout the history of Asteraceae. *Proc. Natl. Acad. Sci. USA* 116: 14083–14088.

Panero, J.L., Freire, S.E., Espinar, L.A., Crozier, B.S, Barboza, G.E. & Cantero, J.J. 2014. Resolution of deep nodes yields an improved backbone phylogeny and a new basal lineage to study early evolution of Asteraceae. *Mol. Phylogenet. Evol.* 80: 43–53.

Tournefort, J.P. de. 1700. Institutiones Rei Herbariae, 3 vols. Paris: Typographia Regia.

Vaillant, S.1721. Établissement de nouveaux caractères de trois familles ou classes de plantes à fleurs composées; sçavoir, des Cynarocéphales, des Corymbifères et des Cichoracées. *Hist. Acad. Roy. Sci. Mém. Math. Phys. (Paris)* 7–8: 174–224.

Taraxacum F.H.Wigg. (Cichorieae) in Australia:

The story of systematic research on the island continent in the last four decades

Robert F. Parsons

Department of Environment and Genetics, La Trobe University, Bundoora VIC 3086, Australia
r.parsons@latrobe.edu.au

DOI: http://dx.doi.org/10.53875/capitulum.03.2.02

ABSTRACT

The first *Taraxacum* species to be described from Australia was the native *T. cygnorum*, published by Handel-Mazzetti in 1907. After this, there was no botanical publication on *Taraxacum* in Australia, either native or alien, until the second and so far only other known native, *T. aristum*, was described in 1964. No further *Taraxacum* work occurred until 1983, when N. H. Scarlett began his nearly 40 years of intensive work on both native and alien *Taraxacum* species. He made the first records of *T. cygnorum* since 1907 and raised progeny of both native species for the first time. This, and other detailed work, was indispensable to the description of the new *Taraxacum* sect. *Australasica* Kirschner, Scarlett & Stepanek. Regarding naturalized plants, Scarlett was eventually able to identify 29 species from five different sections, but scores more species remain to be thus recognized. This whole episode demonstrates how the progress of plant systematics research can be highly piecemeal and intermittent when it involves a large, difficult genus in a botanically under-resourced country.

Keywords: electronic floras, historical taxonomy, naturalized weeds, *Taraxcum* sect. *Australasica*.

A RECENT EPISODE OF *TARAXACUM* RESEARCH IN AUSTRALIA

Taraxacum F. H. Wigg (Dandelions; Cichorieae) is a genus of about 2,500 species and microspecies in *ca.* 58 sections (Kirschner et al., 2020) which are mostly native to Eurasia. Hundreds of these species have become naturalized in temperate and boreal areas around the world, often occurring in ruderal sites and as economically important weeds.

Australia's first flora (Bentham, 1866) records a single *Taraxacum* taxon, a Eurasian aggregate still often called *T. officinale* F. H. Wigg. It was not until Cooke (1986) that a second naturalized taxon, *T. erythrospermum* Andrz. ex Besser was recorded. The subject of naturalized *Taraxacum* microspecies is returned to below.

Turning to *Taraxacum* taxa native to Australia, the first such record is the description of *T. cygnorum* Hand.-Mazz. in 1907 (Figure 1). Not until 1964 was the second native *T. aristum* G.E.Haglund & Markl. described, which later became the first native *Taraxacum* to be included in an Australian flora (Willis, 1973). The genus remained virtually ignored taxonomically in Australia until 1983 when Neville H. Scarlett of La Trobe University, assisted by the present author (RFP), began serious systematic work on it. Significantly, Scarlett re-discovered and re-collected the native *T. cygnorum* which had not been seen since the type collection of 1907.

There were numbers of specimens of the other native, *T. aristum*, in Australia herbaria, but only one had been recognized as *T. aristum*, in this case by Willis (1973). Scarlett found, recognized, collected

Table 1. Sections, microspecies and their native range of *Taraxcum* taxa in Australia. The species records from Australia are from Scarlett (2023); the European section names and native ranges are from Kirschner et al. (2007+).

Section	Microspecies	Native range
Taraxacum sect. ***Australasica*** Kirschner, Tenney & Štěpánek	*T. cygnorum* Hand.-Mazz.	S. Australia
	T. aristum G.E.Haglund & Markl.	SE. Australia
Taraxacum sect. ***Erythrosperma*** (H.Lindb.) Dahlst.	*T. gracilens* Dahlst.	S. Europe
	T. sarcidanum Arrigoni	Sardinia
	T. gasparini Tineo ex Lojac.	S. Europe
	T. hepaticolor Soest	Iran
	T. muttidentatum Soest	S. Europe
	T. lambinonii Soest	S Europe
	T. simile Raunk	NW. & W. Europe
Taraxacum sect. ***Hamata*** H. Øllg.	*T. hamatulum* Hagend., Soest & Zevenb.	NW. & W. Europe
	T. hamiferum Dahlst.	N. & C. Europe
	T. kernianum Hagend., Soest & Zevenb.	C. Europe
	T. pruinatum M. P. Christ.	N. & C. Europe
	T. spiculatum M. P. Christ.	N. & C. Europe
	T. subericinum Hagend., Soest & Zevenb.	N. & C. Europe
Taraxacum sect. ***Celtica*** A.J.Richards.	*T. akteum* Hagend., Soest & Zevenb.	Netherlands, Great Britain
	T. bracteatum Dahlst.	NW. & W. Europe, Great Britain
	T. subbracteatum A. J. Richards	Great Britain
Taraxacum sect. ***Mexicana*** A.J.Richards.	*T. submolle* A. J. Richards	C. America & Haiti
Taraxacum sect. ***Taraxacum*** F. H. Wigg	*T. acrophorum* G. E. Haglund	N. & C. Europe
	T. aequilobium Dahlst.	N. & C. Europe
	T. ericinoides Hagend., Soest & Zevenb.	Germany
	T. khatoonae Abedin	W. Himalayas of India
	T. oblongatum Dahlst. ex Druce	N., C., S. Europe & Great Britain
	T. ohritense Sonck	Albania
	T. pachymerum G. E. Haglund	N. & C. Europe
	T. polyodon Dahlst.	N. & C. Europe
	T. prionum Hagend., Soest & Zevenb.	C. Europe, Great Britain
	T. quadrangulum Railons.	N. & C. Europe
	T. squamulosum Soest	Corsica
	T. retzii Soest	S. Europe, Great Britain
	T. skanderbegii Sonck	Albania
	T. subhuelphersianum M.P.Christ.	N. & C. Europe

Figure 1. The Australian native species *Taraxacum cygnorum* near Cape Nelson, Victoria. *Photo by John Eichler.*

and raised progeny of a series of plants in the 1980s. These new collections and progeny of both species were indispensable to the description of a new section, *Taraxacum* sect. *Australasica* Kirschner, Tenney & Štěpánek which thereby was separated from the South American *T.* sect. *Antarctica* Hand.-Mazz. and is made up of the Australian species and *T. zealandicum* Dahlst., the only New Zealand native *Taraxacum* (Uhlemann et al., 2004). *Taraxacum* sect. *Australasica* is distinguished from most other sections by having outer involucral bracts appressed against the capitulum instead of spreading. It can be distinguished from *T.* sect. *Celtica* by having a white margin on the outer involucral bracts, and by the ligules not or barely exceeding the length of the involucre (Figure 2).

The genus *Taraxacum* is known for its variation in breeding systems and for the large number of 'microspecies'. Only about 10% of the species are self-compatible or self-incompatible-allogamous sexual diploids, including the three species in *T.* sect. *Australasica* (Scarlett, 2015). Most species, however, are polyploid (usually triploid) and apomictic. Their apomixis is autonomous, meaning that they do not require pollination even to develop the endosperm (van Dijk et al., 2003). Conversely, apomictic, polyploid plants produce some diploid,

Figure 2. A. Capitulum of *Taraxacum aristum* (L.G. Adams 2636, CANB 252303) showing key characters of *Taraxacum* sect. *Australasica*; red arrow indicates the appressed outer phyllaries with scarious white margin; dotted lines indicate ligules barely exceeding the phyllaries. **B.** *Taraxacum hamatulum* (N.H. Scarlett s.n., CANB 883565); red arrow indicates the reflexed outer phyllaries; dotted lines indicate longer ligules typical of most species of the genus. *Photos by Alexander Schmidt-Lebuhn.*

Unveiling the Dandelion

Dandelions are one of the most familiar genera of Compositae, but other Cichorieae are often confused for them. Dandelions are characterized by solitary capitula on leafless stems, a differentiation of the involucre into inner and outer bracts, cypselae with a long beak, and a multiseriate, finely barbellate pappus. The apical portion of the seed-bearing part of the cypsela, just under the beak, is often called the 'cone' and its shape is a character useful for species identification, as is the ornamentation of the cypsela surface.

A member of T. sect. Taraxacum, Canberra, Australia.
Photo by Alexander Schmidt-Lebuhn

functional pollen that can cross with sexual, diploid species to produce new triploids, who inherit apomixis as a dominant trait (Mártonfiová, 2015). In this way, numerous apomictic 'microspecies' have been created through repeated crosses between apomictic and sexual plants, including all species that are introduced to Australia.

Simultaneously to this work, Scarlett began to identify *Taraxacum* microspecies introduced to Australia; these were hitherto treated in Australia simply as two aggregate taxa, *T. officinale* and *T. erythrospermum* (see above). By 2015, he had identified 13 alien taxa to already-described species in four different sections, and his account was published in the Flora of Australia (Scarlett, 2015).

Scarlett's following flora account was for the state of Victoria (Scarlett, 2019), adding the names of further alien species. Following his death in 2022, that account has been combined with his earlier work on the other Australian states in the periodically updated eflora version of the Flora of Australia (Scarlett, 2023) which includes only minor changes since his death.

The final tally of his additions to the naturalized flora stands at 29 taxa from 5 sections (Table 1), but scores more microspecies remain to be recognized.

The source areas of the identified alien taxa (Table 1) clearly show the huge predominance of apomictic microspecies of European origin. Also, the data for the three most common European sections show the well-known climate correlation between the predominantly northern European *T.* sect. *Hamata* H. Øllg. and the temperate European to Central Asian *T.* sect. *Erythrosperma* (H.Lindb.) Dahlst.. There are a few taxa in Australia of restricted native range in Europe (Albania, Corsica and Sardinia) and, more strikingly, a single taxon from areas remote from Europe (Central America, Iran and the Himalayas). Further interpretation must await future data (Lenzner et al., 2022).

The background to Scarlett's work was that he was working on the second-largest genus in the tribe Cichorieae, of about 2,500 species and microspecies, many of them apomictic and taxonomically difficult; accordingly, it was essential for him to correspond with European experts, in his case, Antonio Galán de Mera in Madrid, Jan Kirschner and his group in Pruhonice, Czech Republic and Ingo Uhlemann in Dresden. Scarlett himself had completed an excellent plant systematics course for his B.Sc. degree. He worked mostly alone; his great ability to work successfully on one of the most taxonomically difficult angiosperm genera was largely due to an exceptional innate ability to recognize significant differences between plants both in the herbarium and in the field.

Unusually, Scarlett faced a task where a large, weedy genus had become prominent in the Australian flora, yet more than 150 years since the publication of the first flora there (Bentham, 1866), the alien *Taraxacum* flora was known by just two aggregate taxa. After his 40 years of single-handed research, 29 taxa are now known to microspecies level but scores more species remain to be recognized. It is to be hoped that his project exploring which *Taraxacum* species are naturalized in Australia will be continued by others.

ACKNOWLEDGEMENTS

I thank Dr. Phillip Kodela and Valentino Stajsic for invaluable advice on *Taraxacum* systematics and Australian flora publishing and Dr. Alexander Schmidt-Lebuhn and Dr. Ingo Uhlemann for critical comments and advice on manuscript preparation.

LITERATURE CITED

Bentham, G. 1866. *Flora Australiensis*, vol. 3. London: Reeve & Co.

Cooke, D. A. 1986. *Taraxacum*. Pp. 1655-1656 in Jessop, J. P. & Toelken, H. R., (eds.) *Flora of South Australia*, 4th edn, vol.3. Adelaide: Govt. Printer.

Kirschner J., Štěpánek J. & Greuter W. 2007+. *Taraxacum*. – In Greuter, W. & Raab-Straube, E. von (Ed.): Compositae. – Euro+Med Plantbase – the information resource for Euro-Mediterranean plant diversity. http://ww2.bgbm.org/EuroPlusMed

Kirschner, J., Štěpánek, J., Klimeš, L., Dvorský, M., Brůna, J., Macek, M., & Kopecký, M. 2020. The *Taraxacum* Flora of Ladakh, with notes on the adjacent regions of the West

Himalaya. *Phytotaxa* 457: 1–409. https://doi.org/10.11646/phytotaxa.457.1.1

Lenzner, B., Latombe, G., Schertler, A., Seebens, H., Yang, Q., Winter, M., Weigelt, P., van Kleunen, M., Pyšek, P., Pergl, J., Kreft, H., Dawson, W., Dullinger, S., & Essl, F. 2022. Naturalized alien floras still carry the legacy of European colonialism. *Nat. Ecol. Evol.* 6: 1723–1732. https://doi.org/10.1038/s41559-022-01865-1

Mártonfiová, L. 2015. Hybridization in natural mixed populations of sexual diploid and apomictic triploid dandelions (*Taraxacum* sect. *Taraxacum*): Why are the diploid sexuals not forced out? *Folia Geobot*. 50: 339–348. https://doi.org/10.1007/s12224-015-9231-y

Scarlett, N. H. 2015. *Taraxacum*. Pp. 95-112 in Wilson, A. (ed.) *Flora of Australia*, vol.37.[hardcopy]. Melbourne:ABRS/CSIRO.

Scarlett, N. H. 2019+[continuously updated]. *Taraxacum* in *VicFlora* (Royal Botanic Gardens: Melbourne). [https://vicflora.rbg.gov.au]

Scarlett, N. H. 2023. [continuously updated]. *Taraxacum*, in *Flora of Australia* (Australian Biological Resources Study: Canberra). [https://profiles.ala.org.au/opus/foa/profile/Taraxacum]

Uhlemann, I., Kirschner, J. & Štěpánek, J. 2004. The genus *Taraxacum* (Asteraceae) in the southern hemisphere. I. The section *Antarctica* Handel-Mazzetti and notes on dandelions of Australasia. *Folia Geobotanica* 39: 205-220.

van Dijk, P.J., van Baarlen, P., & de Jong, J.H. 2003. The occurrence of phenotypically complementary apomixis-recombinants in crosses between sexual and apomictic dandelions (*Taraxacum officinale*). *Sex. Plant Reprod.* 16: 71–76. https://doi.org/10.1007/s00497-003-0177-5

Willis, J. H. 1973. *Taraxacum*. Pp. 771-772 in *A Handbook to Plants in Victoria*, vol. 2. Melbourne University Press.

Charles Jeffrey:
polyglot, synantherologist and cucurbitologist

D. J. Nicholas Hind

The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, UK; *n.hind@kew.org*

DOI: http://dx.doi.org/10.53875/capitulum. 03.2.03

ABSTRACT

This article commemorates the life and career of Charles Jeffrey (10th April 1934– 29th March 2022), a preeminent botanist renowned for his contributions to plant systematics, particularly in the families Cucurbitaceae and Compositae. The text interweaves personal anecdotes, professional achievements, and insights into Jeffrey's enduring legacy in taxonomy, nomenclature, and conservation. Jeffrey's extensive career included his tenure at the Royal Botanic Gardens, Kew, where he mentored the author and other colleagues, as well as his post-retirement work at the Komarov Botanical Institute in St. Petersburg. Key highlights include Jeffrey's pioneering systematic frameworks, his involvement in global conferences, and his significant role in the translation of Armen Takhtajan's seminal work on angiosperm origins. His contributions are further exemplified by a detailed bibliography and a nomenclator of suprageneric, generic, and infrageneric taxa he published within Cucurbitaceae and Compositae. A comprehensive list of his publications and taxa is presented. This article blends elements of an autobiography, an obituary, and a celebration of Jeffrey's contributions, underscoring his indelible impact on botany and his enduring influence on colleagues and the scientific community.

Keywords: Asteraceae, bibliography, biography, Compositae, Cucurbitaceae, taxonomy.

INTRODUCTION

When I joined the staff in the Herbarium of the Royal Botanic Gardens, Kew in late 1985, Charles Jeffrey (Figure 1) was my boss and mentor for the first nine years of my career, and the last nine years of his. It was my role, according to my former Head of Department, Prof. Gren Lucas (the Keeper of the Herbarium) to "learn how Charles worked" ...! A tall order, and to do so with such a pre-eminent specialist like Charles, especially someone with a photographic memory. Charles was exceptionally generous with his time for a fledgling synantherologist.

Throughout the time we worked together I never ceased to be amazed at Compositae family sorts, especially involving African material, when Charles and Gerald Pope would discuss the finer points of determining material to subspecific or varietal level. Or, Charles, with his main interests in Africa and Asia, walking through 'the Old Library' (now the Guild Room) in Hunter House, whilst a Brazilian general family sort was underway – and being able to name much material to genus at a mere glance. The 'Compositae sub-section' (as he christened it), with one assistant, and myself, Gerald (then Editor of Flora Zambesiaca) and Charles, would often set too

Figure 1. A young Charles, in his Sidney Sussex College blazer and stripe. *Photo courtesy of Helen and Linda Jeffrey*.

and all get involved in basic curatorial tasks. It didn't matter whether that was laying away new accessions, moving whole blocks of material so as to ease up space on either the ground or first floor (or both) in Wing B, or getting to grips with a generic revision and the curatorial 'nitty gritty'. I think we worked well together as there was little we couldn't discuss, and he culminated my mentorship by overseeing a fortnight of the 'International Compositae Conference, Kew, 1994', in July. Never one for great, or any, ceremony, Charles left Kew, after a very succinct meeting (of only seven people) in the Keeper's office, at the end of October of 1994 offering few words; he departed for St. Petersburg the following week, having officially retired on 31st October. He left me in charge of his reliquae (some 15 large boxes of books, mostly in Russian), his old tea mug, and a dud battery-operated wall clock; the boxes remain sealed!

Throughout his retirement Charles continued working. I would receive his handwritten letters at regular intervals (the envelopes littered with as many Russian stamps as Charles could find), often with requests for copies of papers that he couldn't find in the Komarov library. Occasionally there would be missives on how he perceived things were/weren't going, these usually following up on news I'd sent him on how things were progressing, or otherwise, in Kew. There would often be an unplanned annual meeting with him, invariably in the Library Stacks at Kew, Charles having come over from Russia with Margarita to renew his visa, and taking the opportunity to check on various references. However, post-Kubitzki (a volume edited entirely long-hand, on paper, by the way, much to co-editor Joachim's chagrin I suspect), Charles carried on with his own research, often helping Margarita with hers.

During the last few years of his life, and seeing the demise of several of his former colleagues, I managed to twist his arm to consider getting some notes together for a short autobiography, or sufficient for me to write an obituary (or two). Several sheets of handwritten notes later (with most of the references, only lacking their titles, jotted down from memory!) he sent a letter with the end result. He had been concluding a script on *Cucumis* in May of 2021 and Charles's last 'opinion piece' (dating from June 2021) was a 'legacy or perhaps swan-song' on the Senecioneae (which he left to me to decide what to do with). He was still corresponding with me until late January of 2022, and his death came as a shock. Helen Jeffrey (one of his daughters) contacted me on 10th April (on what would have been his birthday) to inform me of his demise. Sadly, after admission to hospital in St Petersburg on 17th March 2022, Charles died on 29th March. Unfortunately, COVID-19 regulations were in full force and Margarita was not allowed to visit the hospital. Charles was laid to rest in the Pargolovo Village, Northern Cemetery, to the north of St. Petersburg. Charles leaves three children by his first wife (Ruth), Helen, Linda and Martin, and six grandchildren – two each! My condolences remain with Margarita.

The following is a combination of Charles's short autobiography, and a part-formal obituary, including a detailed bibliography, and a nomenclator of the suprageneric, generic and infrageneric taxa published by Charles in both the Cucurbitaceae and Compositae; a similar nomenclator for specific and infraspecific taxa would be too long a list.

ABOUT CHARLES

Charles was born in London (10th April 1934), where his father was a fireman during the Second World War. From his mother (Lilian May) he acquired a love of vocal and especially operatic music, from his father (Charles Sydney) a keen interest in gardening and natural history, which no doubt helped to determine his future career. He was fortunate to spend his childhood in Walthamstow, right on the edge of Epping Forest, which soon became his boyhood haunt and joy. He was a pupil at Sir George Monoux Grammar School (converting to first to a Sixth Form College and incorporated as Sir George Monoux College in 1993), Chingford Road, Walthamstow, where, in the summer of 1952, he 'attained the pass standard' at the University of London General Certificate of Education examination in Physics, Chemistry and Zoology (Advanced) and Botany (Ordinary). Other interests, outside of the field of science, included literature (especially Shakespeare and his contemporaries), railways, cats, football and track-and-field athletics. He was also a member of The Surrey Trust for Nature Conservation. After National Service, during which for 18 months he studied Russian at the Joint Services School for Linguistics, he entered Sidney Sussex College, University of Cambridge (Figure 2) and, on graduating in 1957, accepted a (then Colonial Office) post as a taxonomist at the Royal Botanic Gardens, Kew, where he remained until his retirement in 1994. He then moved to St Petersburg and until 2006 worked in association with the Komarov Botanical Institute.

Five main areas of interest may be discerned in Charles's published works (these are listed in the bibliography at the end) – systematics of Cucurbitaceae (1), systematics of Compositae (2), systematics of higher taxa (inter alia proposing the now universally accepted concept he called Streptophyta for the great lineage of Chlorobionta that includes the zygophytes, chlorophytes, Culeochaetes and embryophytes (3), taxonomic theory and nomenclature (4), and the conservation of nature and natural resources (5). The experience of many years teaching systematics to Kew's horticultural students is embodied in his introductory work on plant taxonomy (6). Charles was a founder member of the Conservation Society (now the Conservation Trust) and for many years was a supporter of the Field Studies Council.

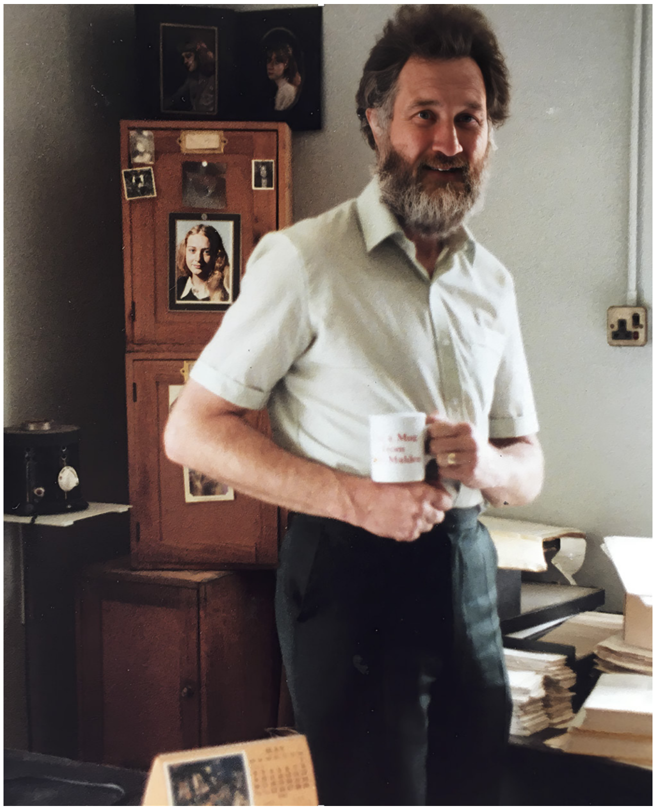


Figure 2. Charles in his office, top floor, Wing A, the Herbarium, RBG, Kew, in the 1980s. *Photo courtesy of Helen and Linda Jeffrey.*

In the course of his scientific work, Charles visited every continent except Antarctica, taking part in conferences or congresses in England, Scotland, Germany, Belgium, Holland, Spain, Australia, Canada, the USA, China, Russia, and Japan, and collecting in Gabon (1957) (Figure 3), the Seychelles (1962-63)(7), Kenya (1963), Mongolia (1970) and Venezuela (1977). [Members of the University of Cambridge Gabon expedition included J. M. G. Davis (of Gonville and Caius college), M. Hayward (of Gonville and Caius college), J. Anton-Smith (of Gonville and Caius College), C. Jeffrey and D. Pomeroy (of Sidney Sussex College) and J. Davies (of St Catharine's College).] Among the conferences he helped to organize were those on the biology and utilization of the Cucurbitaceae (Ithaca, New York, 1980) and on the systematics, biology and utilization of the Compositae (Kew, 1994) in which 22 botanists from the countries of the former Soviet Union took part. Charles's connection with that country began in 1966, when he visited St

A Compositae Champion

Charles, in preparation for a 'country walk' in the 1970s

Photo courtesy of Helen and Linda Jeffrey

Figure 3. The 'Gabon Crew', from 1957. Guess which is Charles?!

Petersburg (then Leningrad) and Tashkent to study *Bryonia* and prepare a translation of a revised and augmented version of the second (1961) edition of Armen Leonovich Takhtajan's *Origin of Angiosperm Plants* (8). In 1977 he played a key role in securing for the Komarov Botanical Institute grants totalling $1 million for renovation of its herbarium and library building. Perhaps fittingly, his last publication was an obituary of Armen Takhtajan (9).

CHARLES' REMINISCENCES & ANECDOTES

Charles noted that his first publications were Aizoaceae *sensu lato*, for the Flora of Tropical East Africa (FTEA), and a precursor paper in Kew Bulletin.

"I've also done a few odd jobs, e.g. Sapindaceae and Thymelaeaceae for my (as in DJNH) bugbear (i.e. Flora of Iraq) and a revision of Polygonatum in E. Asia. When the FTEA staff was transferred to the Ministry of Agriculture, Fisheries, and Food (MAFF) at Kew, I was put formally in charge of areas 3 & 4, although I continued to work on FTEA. How did I come to work on Cucurbits and Comps? Well, purely by chance. The people who were supposed to do these families for FTEA had decamped to (hopefully) greener pastures and there remained an enormous backlog of un-named specimens for these two 'orphan' families. Edgar Milne-Redhead, then in charge of the African section, just detailed me to do these jobs – the results you know."

"Another amateur interest is mycology, and I always enjoyed taking part in fungal forays. In fact,

I applied unsuccessfully for a MAFF post at Kew in the Mycology Section before applying for and obtaining the FTEA post, in favour of which I turned down an offer of a post in plant pathology at East Malling Research Station and an offer to work in palaeobotany at Reading University with Tom Harris."

One of Charles's favourite pastimes was country walking, or rambling as it is sometimes called (see image on page 49], first in S W Essex (centered on Epping Forest), then when living in New Malden on the chalk and greensand of Surrey and W Sussex, and generally in the mountains of the SW Scottish Highlands (the hinterland of Oban), the Lake District, and especially N Wales, where he walked all the peaks over 3000', the Moelwyns and his favourite mountain Moel Siabod; there he also once did a mountain marathon (where are those legs now?).

"*North Wales also houses many examples of another of my passions – narrow gauge steam railways*"

Charles was a life member of the Welsh Highland Light Railway, Porthmadog, Wales.

"As for anecdotes, well, just a few. When I came to Leningrad in 1966, the people at the Komarov had kindly booked me into an inexpensive hotel conveniently situated for travel to the institute. But I spent only one night there. The powers that be ruled that foreigners, especially capitalists like me, must stay in a more expensive hotel with a section especially put aside for them. So I had to move to the less conveniently situated 'Astoria'. The Komarov people had just overlooked this rule."

"A couple of anecdotes about China, 1980. The country had only just opened up to foreigners and there was a severed shortage of "interpreter-guides-policemen". When in Wuhan, I was allocated such a "keeper" and it soon became obvious that he knew very little English. "For what language are you really an interpreter?" I asked. "Russian" he replied. "No problem", said I. So we conversed in Russian for the few days I was in that city. Another demonstrates the flexibility of the Chinese language. From mainland China I went to Taiwan via Hong Kong. Taiwan would not admit you if you had a mainland China stamp in your passport, and vice versa. So for this trip I was provided with two UK passports. On arrival in Taipei, I was at first puzzled by the street signs, until I realized that in mainland China, the ideograms had to be read from left to right, but in Taiwan, from right to left."

"A trip across the Irish Republic in 1956, to record plant distributions for the "Atlas of the British Flora" project provided of course (this being Ireland) some wry moments. At one pub, we arrived late and the landlord would not open the door for us. "If I let you in,", he said, "the police will see and I would lose my licence". "You must come in by the back door." At another pub, one end of the bar was so high that even I, the tallest member of our party, found it difficult to place my glass upon it. "Why is it so high?" we asked. In reply we were told "the floor sank". One day we were looking for a place to camp and found a convenient field. On asking the farmer for permission he said "No, you cannot camp here, we have a very dangerous bull that might take exception to your

Figure 4. Charles and Margarita, in Richmond, December 2016. *Photo courtesy of Helen and Linda Jeffrey.*

tent." we thought this was just a load of "bull" to refuse us permission, but he said "look, over there", and true to tell, we saw an enormous bull in the next field. "But" we said, "We see you have a bull pen – why can't he be in there?" "Oh, ", the famer replied, he (the bull) can't stand being penned up. But if you care to camp in the bull pen, you would be safe". So there we camped for the night.

"I also enclose a short biographical note published in 2005, which provides some other details [not least that Charles married Margarita Baranova on 17th September 2001, {at the Wedding Palace No. 2}, some 35 years to the day after they met – whilst Charles was researching on Bryonia (Cucurbitaceae) in the Komarov Institute and the Vavilov Institute of Plant Industry!] (Figure 4). I may add that in my time, I have served on a number of nomenclatural committees, for 1994-2006 I was a member of the editorial board of Botanicheskii Zhurnal and to this day am still a member of the editorial board of Genetic Resources and Crop Plant Evolution.

"Looking back, I consider that I was very fortunate to have such a varied and interesting career, and to have worked at Kew under mainly sympathetic governments and with adequate financing. Now we have an English Trump as P.M., much to the chagrin of the land (Scotland) of my father's ancestors and things can only get worse. If I make 90, you can publish your piece as a celebratory contribution, not as a wake.

"With all best wishes from myself and Margarita.

"Charles."

[June 2021]

ACKNOWLEDGEMENTS

Clearly, the most conspicuous acknowledgement should be to Charles Jeffrey himself, as my patient line manager for nine years, correspondent for the last 27, and especially in supplying his handwritten short autobiography. I would also like to thank Helen, Linda and Martin Jeffrey in making a number of family photographs available for me to select from for this, and other (see Renner & Hind 2023), obituaries of their father. Last but not least, I would like to thank Margarita for being Charles's companion for the last 26 years, and for them both for being such generous hosts during a visit to St. Petersburg in 1998 (and Margarita's late brother, an Academician of the Russian Academy of Sciences, for ensuring a memorable evening at the opera – in the 'type locality' for Tchaikovsky's *Eugene Onegin*).

BIBLIOGRAPHY

References arranged in chronological order under subject areas annotated in text. References marked with an '', are those added by DJNH in line with the subject areas.*

1 – Systematics of the Cucurbitaceae, etc.

*__Jeffrey, C.__ 1961. Aizoaceae (including Molluginaceae and Tetragoniaceae). In: G. Ll. Lucas, R. Polhill & E. Milne-Redhead (eds), *Flora of Tropical East Africa*. Balkema. pp. 37.

Jeffrey, C. 1962 Notes on Cucurbitaceae, including a proposed new classification of the family. *Kew Bull*. 15(3): 337–371.

*__Jeffrey, C.__ 1962. The application of the generic names *Anguria* and *Elaterium* (Cucurbitaceae). *Kew Bull*. 16(2): 197–198.

Jeffrey, C. 1964. (Review) *Cucurbits: Botany, Cultivation and Utilization* – T. W. Whitaker & G. L. David. *Kew Bull*. 17(3): 397–399

*__Jeffrey, C.__ 1964. (Review) The taxonomy displayed. Plant taxonomy: Methods and Principles – L. Benson. *Kew Bull*. 17(3): 441–445.

Jeffrey, C. 1964 A note on pollen morphology in Cucurbitaceae. *Kew Bull*. 17(3): 473–477.

Jeffrey, C. (Oct. 1964). Key to the Cucurbitaceae of West Tropical Africa, with a guide to localities of rare and little-known species. *J. W. Afr. Sci. Assoc*. 9(2): 79–97.

Jeffrey, C. 1965. Further notes on Cucurbitaceae. *Kew Bull*. 19(2): 215–223.

Jeffrey, C. 1967. Cucurbitaceae. In: G. Ll. Lucas, R.M. Polhill & E. Milne-Redhead (eds), *Flora of Tropical East Africa*. Crown Agents for Overseas Governments and Administrations, London/Balkema. pp. 156.

Keraudren, M. & Jeffrey, C. 1967. Le genre *Raphidiocystis* (Cucurbitaceae) en Afrique et à Madagascar. *Bull. Jard. Bot. État Bruxelles* 37(3): 319–328.

Jeffrey, C. 1969. A review of the genus *Bryonia* L. (Cucurbitaceae). *Kew Bull*. 23(3): 441–461.

Jeffrey, C. 1971. Tabulae 3661, 3662, 3664, 3664. *Mukia javanica*, *M. maderaspatana*, *M. leiosperma* & *M. celebica*. *Hooker's Icon. Pl.* 37: Tabulae 3661, 3662, 3663, 3664 & 1 – 12.

Jeffrey, C. 1971. Further notes on Cucurbitaceae: II. The tribe Cucurbiteae. *Kew Bull*. 25(2): 191–236.

Jeffrey, C. 1972. Cucurbitaceae. In: P. H. Davis, D. F. Chamberlain & V. A. Matthews (eds), *Flora of Turkey and the East Aegean Islands* 4: 200–208.

***Jeffrey, C.** 1975. Further notes on Cucurbitaceae: III – Some Southern African taxa. *Kew Bull*. 30(3): 475–493.

Jeffrey, C. 1975. A palyno-taxonomic study of *Peponium* (Cucurbitaceae). *Kew Bull*. 30(3): 495–502.

Jeffrey, C. 1978. Further notes on Cucurbitaceae: IV – Some New-World taxa. *Kew Bull*. 33(2): 347–380.

Jeffrey, C. 1978. Cucurbitaceae. In: E. Launert (ed. in chief), J. P. M. Brenan, E. Launert, A. Fernandes & H. Wild (eds), *Flora Zambesiaca: Mozambique, Malawi, Zambia, Rhodesia, Botswana*. Vol. 4. Flora Zambesiaca Management Committee, Royal Botanic Gardens, Kew. pp. 414 449.

Jeffrey, C. 1980. *Cucurbitaceae of Eastern Asia: a report on studies made during, and in connexion with a visit to China, Hong Kong and Japan in 1980*. Royal Botanic Gardens, Kew. pp. 1–60.

Jeffrey, C. 1980. A review of the Cucurbitaceae. *Bot. J. Linn. Soc*. 81(3): 233–247.

Jeffrey, C. 1980. Further notes on Cucurbitaceae: V – The Cucurbitaceae of the Indian subcontinent. *Kew Bull*. 34(4): 789–809.

Chakravarty, H. L. & Jeffrey, C. 1980. Cucurbitaceae. In: C. C. Townsend & E. Guest (eds), *Flora of Iraq* 4. Ministry of Agriculture & Agrarian Reform, Republic of Iraq. pp. 191–208.

Jeffrey, C. 1990. Systematics of the Cucurbitaceae. In: D. M. Bates, R. W. Robinson & C. Jeffrey (eds), *Biology and Utilization of the Cucurbitaceae*. Comstock Pub. Associates, Ithaca, NY. pp. 449–463.

Jeffrey, C. 1982. Further notes on Cucurbitaceae: VI – Cucurbitaceae of the Indian subcontinent: Corrigenda and addenda. *Kew Bull*. 36(4): 789 – 748.

Jeffrey, C. & Trujillo, B. 1992. Cucurbitaceae. In: B. Trujillo (ed.), *Flora of Venezuela* 5(1). pp. 11 – 201. [Originally issued as a pre-print in a spiral binding in 1983].

Jeffrey, C. 1995. Cucurbitaceae. *Flora Nicaragua. Introducción. Gimnospermas y Angiospermas* (Acanthaceae – Euphorbiaceae). Vol. 85(1). Missouri Botanic Garden Press, St. Louis. pp. 688–717.

Jeffrey, C. & Thulin, M. 1993. Cucurbitaceae. In: M. Thulin (ed.), *Flora of Somalia* Vol. 1. Royal Botanic Gardens, Kew. pp. 216–240.

Jeffrey, C. 1995. Cucurbitaceae. In: S. Edwards, M. Tadesse & I. Hedberg (eds), *Flora of Ethiopia & Eritrea* – Canellaceae to Euphorbiaceae. Vol. 2(2). National Herbarium Addis Ababa, Ethiopia & Department of Systematic Botany, Uppsala, Sweden. pp. 17–59.

Jeffrey, C. 2001. Cucurbitaceae. *Mansfeld's Encyclopedia of agricultural and horticultural crops* (*except ornamentals*). Springer, Berlin, London. 3: 1510–1557.

Jeffrey, C. 2005. A new system of Cucurbitaceae. *Bot. Zhurn*. 90(3): 332–335.

Anmin, L., Luqi, H., Shukin, H. & Jeffrey, C. 2011. Cucurbitaceae. In: W. Zhengyi, P. H. Raven & H. Deyian (eds), *Flora of China* 19: 1–56. Science Press, Beijing & Missouri Botanical Garden Press, St. Louis.

2 – Systematics of the Compositae.

Jeffrey, C. 1966. Notes on the Compositae: I. The Cichorieae in East Tropical Africa. *Kew Bull*. 18(3): 427–486.

Jeffrey, C. 1967. Notes on the Compositae: II. The Mutisieae in East Tropical Africa. *Kew Bull*. 21(2): 177–223.

Jeffrey, C. 1968. Notes on the Compositae: III. The Cynareae in East Tropical Africa. *Kew Bull*. 22(1): 107–140.

Jeffrey, C., Halliday, P., Wilmot-Dear, M. & Jones, S. W. 1977. Generic and sectional limits in *Senecio* (Compositae): I. Progress report. *Kew Bull*. 32(1): 47–67.

Jeffrey, C. 1977. Corolla forms in Compositae – some evolutionary and taxonomic speculations. In: V. H. Heywood, J. B. Harborne & B. L. Turner (eds), *Biology & Chemistry of the Compositae*. Academic Press, London, New York & San Francisco. Vol. 1: 111–118.

Jeffrey, C. 1978. Compositae. In: V. H. Heywood (Cons. Ed.), *Flowering Plants of the World*. Oxford University Press, Oxford. pp. 263–268.

Jeffrey, C. 1979. Generic and sectional limits in *Senecio* (Compositae): II. Evaluation of some recent studies. *Kew Bull*. 34(1): 49–58.

Jeffrey, C. & Yi-Ling, C. 1984. Taxonomic studies on the tribe Senecioneae (Compositae) of Eastern Asia. *Kew Bull*. 39(2): 205–446.

Jeffrey, C. 1986. The Senecioneae in East Tropical Africa: Notes on Compositae: IV. *Kew Bull*. 41(): 873–943.

Jeffrey, C. 1987. Developing descriptors for systematic analyses of Senecioneae (Compositae). *Bot. Jahrb. Syst.* 108(2/3): 201–218.

***Gilbert, M. G. & Jeffrey, C.** 1988. A revision of *Ethulia* (Compositae: Vernonieae). *Kew Bull*. 43(2): 165–193.

Jeffrey, C. 1988. The Vernonieae in East Tropical Africa: Notes on Compositae: V. *Kew Bull*. 43(2): 195–277.

Jeffrey, C. 1992. The tribe Senecioneae (Compositae in the Mascarene Islands with an annotated World Check-list of the genera in the tribe: Notes on Compositae: VI. *Kew Bull*. 47(1): 49–109.

Jeffrey, C. 1993. Senecioneae. In: J. Bosser, J. Guého & C. Jeffrey (eds), Fam. 109. Composées. *Flore des Mascareignes*, La Réunion, Maurice, Rodgrigues. The Sugar Industry Research Institute, Mauritius: L'Institut Français de Recherche Scientifique pour le Développement en Coopération (ORSTOM), Paris: Royal Botanic Gardens, Kew. pp. 130–164.

Jeffrey, C. 1995. Introduction. & Compositae systematics 1975 – 1993. Developments and desiderata. In: D. J. N. Hind, C. Jeffrey, & G. V. Pope (eds), *Advances in Compositae Systematics*. Royal Botanic Gardens, Kew. pp. 1–21.

Kadereit, J. W. & Jeffrey, C. 1996. A preliminary analysis of cpDNA variation in the tribe Senecioneae (Compositae). In: D. J. N. Hind & H. J. Beentje (eds), (D. J. N. Hind, ed.-in-chief), *Compositae: Systematics. Proceedings of the International Compositae Conference, Kew, 1994*. Vol. 1: 349–360. Royal Botanic Gardens, Kew.

Jeffrey, C. 1997. What is *Emilia coccinea* (Sims) G. Don (Compositae)? A revision of the large-headed *Emilia* species of Africa. *Kew Bull*. 52(1): 205–212.

Jeffrey, C. & Beentje, H. J. 2000. Mutisieae, Cynareae, Cichorieae, Vernonieae. In: H. J. Beentje (ed.), *Flora of Tropical East Africa* Compositae (Part 1): 1–285. A. A. Balkema, Rotterdam.

Jeffrey, C. 2001. Compositae. In: R. Mansfeld†, P. H. Hanelt & R. Büttner (eds), *Mansfeld's Encyclopedia of agricultural and horticultural crops* (*except ornamentals*). Springer, Berlin, London. Vol. 4: 2035–2145.

Jeffrey, C. 2002. СИСТЕМАТИКА СЛОЖНОЦВЕТНЫХ В НАЧАЛЕ (COMPOSITAE) XXI ВЕКА. Systematics of Compositae at the beginning of the 21st Century [In Russian]. *Bot. Zhurn*. 87(11): 1–15.

Jeffrey, C. 2004. Systema Compositarum (Asteracearum) nova. *Bot. Zhurn*. 89(12): 1817–1822.

Jeffrey, C. [Dec. 2006](Jan. 2007). In: J. W. Kadereit & C. Jeffrey (vol. eds), K. Kubitzki (ser. ed.), *Families and genera of vascular plants*. VII. 61–87 (Introduction with Key to Tribes); 146–148 (Tribe Gymnarrheneae); 574–575 (Asteroid genus of uncertain placement).

Jeffrey, C. 2005. [Senecioneae] In: H. J. Beentje & S. Ghanzanfar (eds), *Flora of Tropical East Africa.* Compositae (Part 3): 547–548 (generic key to the Senecioneae); 563–617 (*Cineraria* – *Mikaniopsis*); 617–702 (*Senecio* – *Gynura*).

Jeffrey, C. 2009. [Chapter 8] Evolution of Compositae flowers. In: V. A. Funk, A. Susanna, T. F. Stuessy & R. J. Bayer (eds), *Systematics, Evolution, and Biogeography of Compositae*. International Association for Plant Taxonomy, University of Vienna, Austria. pp. 131–138.

Jeffrey, C. 2011. Key to tribes – Senecioneae – *Dicercoclados* (C. Yilin, B. Nordenstam & C. Jeffrey) – Subtribe Tephroseridinae (C. Yilin, L. Ying, Y. Qiner, B. Nordenstam & C. Jeffrey) – *Emilia* (C. Yilin, B. Nordenstam & C. Jeffrey). In: Z. Y. Wu, P. H. Raven & D. Y. Hong (eds), *Flora of China* 20-21 (Asteraceae). Science Press, Beijing & Missouri Botanical Garden Press, St. Louis. pp. 7–8; 373; 435–437; 464–537; 542 543.

3 – Systematics of higher taxa.

Jeffrey, C. 1962. The origin and differentiation of the archegoniate land plants. *Bot. Not*. 115: 446–454.

Jeffrey, C. 1967. The origin and differentiation of the archegoniate land plants: a second contribution. *Kew Bull*. 21(2): 335–349.

Jeffrey, C. 1971. Thallophytes and kingdoms: a critique. *Kew Bull*. 25(2): 291–299.

Jeffrey, C. 1982. Kingdoms, codes and classification. *Kew Bull*. 37(3): 403–416.

4 – Taxonomic theory and nomenclature.

Jeffrey, C. 1967. On the classification of the Cucurbitaceae. *Kew Bull*. 20(3): 417–426.

Jeffrey, C. 1968. Evolution, phylogeny and systematics. *Taxon* 17(1): 65–70.

Jeffrey, C. 1973. *Biological Nomenclature*. [Special topics in Biology series.) E. Arnold, London. pp. 69.

Jeffrey, C. 1976. *Nomenclatura Biológica*. (Spanish translation). Herman Blume Ediciones, Madrid.

Jeffrey, C. 1977. *Biological Nomenclature*. Ed. 2. E. Arnold, London. pp. 72.

Jeffrey, C. 1980. *Biological Nomenclature*, ed. 2. Russian translation.

Jeffrey, C. 1983. (Review). *Advances in Cladistics*, V. A. Funk & D. R. Brooks (eds). – A review. *Kew Bull*. 38(1): 1–10.

Jeffrey, C. 1986. *Tatanama Biologi*. (Malay translation). Dewan Bahasa dan Pustaka Kementerian Pelayaran Malaysia, Kuala Lumpur. pp. 90.

Jeffrey, C. 1989. *Biological Nomenclature*. Ed. 3. E. Arnold, London.

Jeffrey, C. 2003. Phylogenetic trees are not for chopping. *Bot. Zhurn*. 88(2): 1–4.

5 – Conservation of nature and natural resources.

Jeffrey, C. 1970. *Conservation - the Fourfold way*. Conservation Society, Potters Bar. pp. 48.

6 – Introductory work on plant taxonomy.

Jeffrey, C. 1968. *An introduction to plant taxonomy*. Churchill, London. pp. 128.

Jeffrey, C. 1982. *An introduction to plant taxonomy*. Ed. 2. Cambridge University Press, University of Cambridge. pp. 154.

7 – Result of a field trip to the Seychelles.

Jeffrey, C. 1962. *The Botany of the Seychelles: a report by the visiting botanist of the Seychelles Botanical Survey, 1961-2*.

Jeffrey, C. 1968. Seychelles. In: I. Hedberg & O. Hedberg (eds), Conservation of vegetation in Africa South of the Sahara. [Proceedings of a symposium held at the 6th Plenary meeting of the "Association pour lÉtude Taxonomique de la Flore d'Afrique Tropicale" (A.E.T.F.A.T.) in Uppsala, Sept. 12th – 16th, 1966.] *Acta Phytogeogr. Suec*. 54: 275–279.

8 – Translation of Takhtajan's Origin of Angiosperm Plants.

Takhtajan, A. L. 1969. *Flowering plants: Origin and dispersal*. English Translation. Oliver & Boyd, Edinburgh.

9 – Charles' last publication.

Jeffrey, C. 2012. Armen Takhtajan (1910–2009). *Taxon* 61(3): 695–695.

AN EXTENDED BIBLIOGRAPHY

Also found amongst the various bibliographic lists are the following articles and papers by (or on) Charles, in chronological order (doubtless a number might be missing)

Jeffrey, C. 1965. *Artemisia maritima* (Compositae) in the Indian sub-continent. *Kew Bull*. 19(3): 399–400.

Jeffrey, C. 1968. Contributions to the Flora of Iraq: VII. A new species of *Ligia* [sic! = Lygia] Fas. (Thymelaeaceae) from the Middle East. *Kew Bull*. 22(3): 469–471.

Jeffrey, C. 1969. Tab. 549. *Cassinia vauvilliersii*. Compositae. *Curtis's Bot. Mag*. 177(2): Tab. 549.

Jeffrey, C. 1969. Tab. 551. *Prunus hirtipes* vs. 'Semiplana'. Rosaceae. *Curtis's Bot. Mag*. 177(3): Tab. 551.

Boulos, L. & Jeffrey, C. 1969. *Sonchus gigas* and *S. macrocarpus* (Comp.) *Taxon* 18(3): 348–349.

Jeffrey, C. 1969. Tab. 554. *Sorbus* cv. 'Joseph Rock'. Rosaceae. *Curtis's Bot. Mag*. 177(3): Tab 554.

Jeffrey, C. 1970. Tab. 564. *Ursinia chrysanthemoides* cv. 'Geyeri'. Compositae. *Curtis's Bot. Mag*. 177(4): Tab. 564.

Jeffrey, C. 1971. *Vernonia unicata* C. Jeffrey. Compositae: tribus Vernonieae. *Hooker's Icon. Pl*. 7: Tab. 3683.

Jeffrey, C. 1971. Tab. 583. *Chrysanthemum ptarmiciflorum*. Compositae. *Curtis's Bot. Mag*. 178(2): Tab. 583.

Jeffrey, C. 1972. Tab. 595. *Chrysanthemum ferulaceum*. Compositae. *Curtis's Bot. Mag*. 178(3): Tab. 595.

Jeffrey, C. 1973. *Eureiandra leucantha* C. Jeffrey, new Cucurbitaceae from Zambia and Zaïre. *Bull. Jard. Bot. État Belgique* 43(3-4): 425.

Jeffrey, C. 1973. Tab. 654. *Olearia ilicifolia*. Compositae. *Curtis's Bot. Mag*. 179(4): Tab. 654.

Jeffrey, C. 1974. Tab. 665. *Olearia megalophylla*. Compositae. *Curtis's Bot. Mag*. 180(1): Tab. 665, 21–23.

Jeffrey, C. 1974. Tab. 676. *Hirpicium augistifolium*. Compositae. *Curtis's Bot. Mag*. 180(2): Tab. 676, 73–74.

Jeffrey, C. 1974. Tab. 677. *Echinops ruthenicus*. Compositae. *Curtis's Bot. Mag*. 180(2): Tab. 677, 77–81.

Jeffrey, C. 1977. Tab. 728. *Verbesina encelioides*. Compositae. *Curtis's Bot. Mag*. 181(3): tab. 728, 101–103.

Jeffrey, C. 1978. Tab. 755. *Helianthus annuus*. Compositae. *Curtis's Bot. Mag*. 182(1): Tab. 755, 31–34.

Jeffrey, C. (Dec. 1978). (Review). V. H. Heywood, J. B. Harborne & B. L. Turner (eds), *The Biology and Chemistry of the Compositae*. Academic Press, London, New York & San Francisco. 2 vols. *Compositae Newslett*. 7: 1–6.

Jeffrey, C. 1979. A new combination in *Thladiantha* (Cucurbitaceae) for a Chinese medicinal plant. *Kew Bull*. 33(3): 393–394.

Jeffrey, C. 1979. Note on the lectotypification of the names *Cacalia* L., *Matricaria* L. and *Gnaphalium* L. *Taxon* 28(4): 349–351.

Jeffrey, C. 1979 [1980]. The genus *Polygonatum* (Liliaceae) in eastern Asia. *Kew Bull*. 34(3): 435–471.

Jeffrey, C. 1981. Tab. 822. *Helianthus pauciflorus*. Compositae. *Curtis's Bot. Mag*. 183(3): Tab. 822, 115–118.

Jeffrey, C. 1982. Tab. 858. *Hypochaeris oligocephala*. Compositae. *Curtis's Bot. Mag*. 184(2): Tab. 858, 85–87.

Jeffrey, C. 1982. Further note on Eastern Asian *Polygonatum* (Liliaceae). *Kew Bull*. 37(2): 335–339.

Jeffrey, C. 1992. [All Compositae genera]. In: M. Griffiths (ed.), *The New Royal Horticultural Society Dictionary of Gardening* (A. Huxley (ed.-in-Chief)). Vol. 1A–C; Vol. 2D - K; Vol. 3L - Q; Vol. 4R – Z. The Macmillan Press Limited, London; The Stockton Press, New York.

Jeffrey, C. & Hind, D. J. N. 1994. The typification of *Piptolepis* Sch.Bip. (*Compositae*), nom. cons. *Taxon* 43(1): 94–96.

Hind, D. J. N. & Jeffrey, C. 2001. A checklist of the Compositae of Vol. IV of Humboldt, Bonpland & Kunth's *Nova genera et species plantarum*. *Compositae Newslett*. 37. pp. 84.

Anon. [= Jeffrey, C.] 2005. Charles Jeffrey, Legendary Cucurbit Taxonomist. *Cucurbit Network News* (Miami, USA) 12(1): 3.

Baranova, M. A. & Jeffrey, C. 2006. Leaf anatomy and the systematics of the Rhizophoraceae sensu lato. *Bot. Zhurn*. 91(12): 1787–1815.

Renner, S. S. & Hind, D. J. N. 2022. In memoriam Charles Jeffrey (1934-2022). Taxon 71(5): 1135–137.

NOMENCLATOR OF SUPRAGENERIC, GENERA, AND INFRAGENERIC TAXA, PUBLISHED BY CHARLES JEFFREY IN THE COMPOSITAE & CUCURBITACEAE

Compositae (Suprageneric taxa)

Vernonieae subtribe Tephroseridinae C. Jeffrey & Y. L. Chen, *Kew Bull*. 39(2): 207 (1984).

Supersubtribe Eupatoriodinae C. Jeffrey, *Bot. Zhurn*. (Moscow & Leningrad) 87(11): 11 (2002).

Supersubtribe Athroismodinae C. Jeffrey, *Bot. Zhurn*. (Moscow & Leningrad) 89(12): 1820 (2004).

Supersubtribe Bahiodinae C. Jeffrey, *Bot. Zhurn*. (Moscow & Leningrad) 89(12): 1820 (2004).

Supersubtribe Chaenactidodinae C. Jeffrey, *Bot. Zhurn*. (Moscow & Leningrad) 89(12): 1820 (2004).

Supersubtribe Coreopsidodinae C. Jeffrey, *Bot. Zhurn*. (Moscow & Leningrad) 89(12): 1820 (2004), nom. inval.

Supersubtribe Heleniodinae C. Jeffrey, *Bot. Zhurn*. (Moscow & Leningrad) 89(12): 1820 (2004).

Supersubtribe Neurolaenodinae C. Jeffrey, *Bot. Zhurn*. (Moscow & Leningrad) 89(12): 1820 (2004).

Supersubtribe Tagetodinae C. Jeffrey, *Bot. Zhurn*.

(Moscow & Leningrad) 89(12): 1820 (2004).

Supersubtribe Helianthiodinae C. Jeffrey, *Bot. Zhurn.* (Moscow & Leningrad) 89(12): 1821 (2004).

Supersubtribe Madiodinae C. Jeffrey, *Bot. Zhurn.* (Moscow & Leningrad) 89(12): 1821 (2004).

Supersubtribe Milleriodinae C. Jeffrey, *Bot. Zhurn.* (Moscow & Leningrad) 89(12): 1821 (2004).

Supersubtribe Peritylodinae C. Jeffrey, *Bot. Zhurn.* (Moscow & Leningrad) 89(12): 1821 (2004).

Supersubtribe Polymniodinae C. Jeffrey, *Bot. Zhurn.* (Moscow & Leningrad) 89(12): 1821 (2004).

Compositae (Generic, & infrageneric, names)

Piloselloides (Less.) C. Jeffrey, *Kew Bull*. 21(2): 214 (1967), isonym.

Diceroclados C. Jeffrey & Y. L. Chen, *Kew Bull*. 39(2): 213 (1984).

Sinosenecio B. Nord. subsect. *Phalacrocrpa* C. Jeffrey & Y. L. Chen, *Kew Bull*. 39(20: 236 (1984).

Sinosenecio B. Nord. ser. *Scaposi* C. Jeffrey & Y. L. Chen, *Kew Bull*. 39(2): 236 (1984).

Sinosenecio B. Nord. subsect. *Madarogyne* C. Jeffrey & Y. L. Chen, *Kew Bull*. 39(2): 246 (1984).

Sinosenecio B. Nord. sect. *Phyllocaulon* C. Jeffrey & Y. L. Chen, *Kew Bull*. 39(2): 246 (1984).

Sinosenecio B. Nord. subsect. *Lasiogyne* C. Jeffrey & Y. L. Chen, *Kew Bull*. 39(2): 253 (1984).

Sinosenecio B. Nord. ser. *Omnipapposi* C. Jeffrey & Y. L. Chen, *Kew Bull*. 39(2): 253 (1984).

Sinosenecio B. Nord. ser. *Discipapposi* C. Jeffrey & Y. L. Chen, *Kew Bull*. 39(2): 259 (1984).

Sinosenecio B. Nord. ser. *Elati* C. Jeffrey & Y. L. Chen, *Kew Bull*. 39(2): 239 (1984).

Synotis (C. B. Clarke) C. Jeffrey & Y. L. Chen, *Kew Bull*. 39(2): 285 (1984).

Austrocynotis C. Jeffrey, *Kew Bull*. 41(4): 878 (1986).

Kinghamia C. Jeffrey, *Kew Bull*. 43(2): 274 (1988).

Dendrophorbium (Cuatrec.) C. Jeffrey, *Kew Bull*. 47(1): 65 (1992).

Monticalia C. Jeffrey, *Kew Bull*. 47(1): 69 (1992)

Faujasiopsis C. Jeffrey, *Kew Bull*. 47(1): 77 (1992).

Parafujasia C. Jeffrey, *Kew Bull*. 47(1): 79 (1992).

Humbertacalia C. Jeffrey, *Kew Bull*. 47(1): 82 (1992).

Cucurbitaceae (Suprageneric)

Subtribe Acanthosicyoinae C. Jeffrey, *Kew Bull*. 15(3): 339 (1962).

Subtribe Luffeae C. Jeffrey, *Kew Bull*. 15(3): 340 (1962).

Subtribe Ampelosycioinae C. Jeffrey, *Kew Bull*. 15(3): 341 (1962).

Tribe Trichosantheae C. Jeffrey, *Kew Bull*. 15(3): 341 (1962).

Subtribe Herpetosperminae C. Jeffrey, *Kew Bull*. 15(33): 342 (1962).

Subtribe Hodgsoniinae C. Jeffrey, *Kew Bull*. 15(3): 342 (1962).

Subtribe Trochomeriinae C. Jeffrey, *Kew Bull*. 15(3): 342 (1962).

Subtribe Dendrosicyinae C. Jeffrey, *Kew Bull*. 15(3): 344 (1962).

Subtribe Actinostemmatinae C. Jeffrey, *Biol. & Util. Cucurbitac*.: 450 (1990).

Subtribe Cyclantherinae C. Jeffrey, *Biol. & Util. Cucurbitac*.: 461 (1990).

Subtribe Sicyinae C. Jeffrey, *Biol. & Util. Cucurbitac*.: 462 (1990).

Tribe Herpetospermeae C. Jeffrey, *Bot. Zhurn*. (Moscow & Leningrad) 90(3): 333 (2005).

Tribe Luffeae C. Jeffrey, *Bot. Zhurn*. (Moscow & Leningrad) 90(3): 333 (2005).

Cucurbitaceae (Generic)

Myrmecosicyos C. Jeffrey, *Kew Bull*. 15(3): 357 (1962).

Ruthalicia C. Jeffrey, *Kew Bull*. 15(3): 360 (1962).

Sechium P. Browne sect. *Frantzia* (Pittier) C. Jeffrey, *Kew Bull*. 33(2): 361 (1978).

Cucumis L. subgen. *Melo* (Mill.) C. Jeffrey, *Bot. J. Linn. Soc*. 81(3): 238 (1980).

Sinobaijiania C. Jeffrey & W. J. de Wilde, *Bot. Zhurn*. (Moscow & Leningrad) 91(5): 769 (2006).

Pseudocucumis (A. Meeuse) C. Jeffrey, Genet. *Resursy Kul't Rast*.: 174 (2009).

EPONOMY

Jeffreya Wild, *Kirkia* 9(2): 295 (1974). (Compositae)

Neojeffreya Cabrera, *Hickenia* 1(30): 160 (1978). (Compositae)

Jeffreya Cabrera, *Hickenia* 1(23): 125 (1978), nom. illeg., non Wild (= *Neojeffreya* Cabrera)

STYLE

Where art and science converge

THE ILLUSION OF ONE

A lateral view of the secondary head of *Polyachyrus poeppigii* Kunze ex. Less. (Nassauvieae) in Valle del Elqui, Coquimbo region, Chile. Clustering of two or more capitula into secondary heads, or syncephalia, is a trait that occurs in over 70 genera of Compositae and gives the overall inflorescence a flashy appearance without sacrificing the integrity of each individual capitulum.

Isaac Lichter-Marck

THE WARHOL PAPPUS

The pappus of *Rhodanthe spicata* (Steetz) Paul G.Wilson (Gnaphalieae) as seen through an Apexel 200x Mobile LED Microscope Lens.

Alexander N Schmidt-Lebuhn

LOST AMONG A SEA OF STYLES

A bee gathers pollen among the long styles of *Cynara cardunculus* L. (Cardueae)

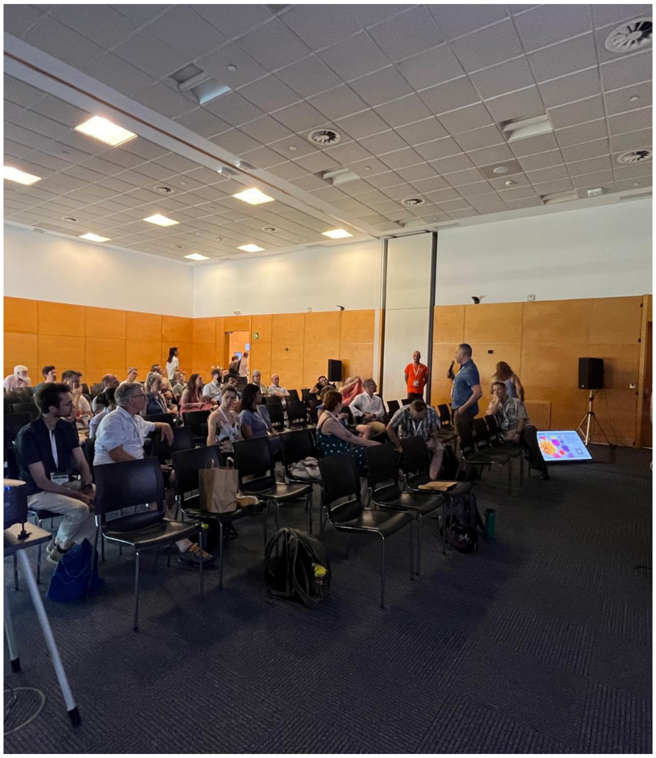
Ary Mailhos

TICATIMES

selected Compositae news and updates from
THE INTERNATIONAL COMPOSITAE ALLIANCE

Edited by Jennifer R. Mandel

JULY 2024



TICA HOSTS SYMPOSIUM AT XX INTERNATIONAL BOTANICAL CONGRESS IN MADRID, JULY 2024

"Synantherology reloaded: Recent advances and the future of evolutionary studies in Compositae" was co-organized by Jennifer Mandel (University of Memphis, USA) Mauricio Bonifacino (Universidad de la República, Uruguay) and featured two sessions with 12 presentations. The symposium highlighted the impact that technological advances in high-throughput sequencing, large-scale phylogenomics, and improved database infrastructure have had on our understanding of the biogeography, systematics, and evolution of the world's largest flowering plant family. The symposium brought together speakers from across career stages and the globe and who presented findings from the past decade including how new data have led to changes in major classification, systematics, biogeography, anatomy, and more in the group we all love.

Magno amore in familiam Synantherearum captus
(Lessing 1829)

SPEAKERS AT TICA SYMPOSIUM:

Dancing with Thistles
Alfonso Susanna, Instituto Botánico de Barcelona, Spain

An updated subtribal classification of Compositae tribe Anthemideae based on extended phylogenetic reconstructions
Christoph Oberprieler, University of Regensburg, Germany

Exploring the Future of Compositae: Advances in Genomics, Transcriptomics, and Functional Genetics
Jennifer Mandel, University of Memphis, USA

Anatomy of Asteraceae: Methodological advances for an old science
Makeli Garibotti Lusa, Universidade Federal de Santa Catarina, Brazil

The Compositae in the Plant and Fungal Tree of Life
Benoit Loeuille, Royal Botanic Gardens, Kew, UK

The Global Compositae Database: challenges and opportunities
Mauricio Bonifacino, Universidad de la República, Uruguay

Phylogenetic insights into the endemic species of the genus Senecio L. (Asteraceae) in India
Akanksha Jeswani, Shivaji University, Kolhapur, India

Biogeography of the Mexico-eastern U.S disjunction in Symphyotrichum
Sushil Dahal, Mississippi State University, USA

Four or more? Integrative species delimitation of the African daisy complex Dimorphotheca pluvialis-sinuata
Thaabiet Parker, South African National Biodiversity Institute, University of Cape Town, South Africa

Phylogenomic insights into the Marguerite daisy tribe (Anthemideae, Asteraceae)
David Criado Ruiz, Real Jadrín Botánico de Madrid-CSIC, Spain

Palynology of Vernonieae from Madagascar (Compositae)
Higor Antonio-Domingues, Royal Botanic Gardens, Kew, UK

Hyperdiverse but still under-explored: recent and future evolutionary studies in the Compositae of Southern Africa
Nicola Bergh, The Compton Herbarium, SANBI Kirstenbosch, Cape Town, South Africa

Screenshot of TICA virtual meeting of December 2024

DECEMBER 2024

WHAT'S NEXT FOR 2025 AND HOW TO GET INVOLVED

TICA also hosted an in-person meeting of more than 40 members at the XX International Botanical Congress in Madrid, Spain. Discussions included a 2nd edition of Systematics, Evolution, and Biogeography of Compositae, the TICATalks virtual seminar series for 2025, the Global Compositae Database (GCD), and CAPITULUM, the official scientific journal of TICA.

In December 2024, nearly 30 people met to form collaborative working groups for these four topic areas. If you are interested in getting involved in one or more of these groups or would be interested in contributing, contact:

TICATalks
Erika Moore-Pollard, ermoore3@memphis.edu,
Carol Siniscalchi, CSiniscalchi@library.msstate.edu

Systematics, Evolution, and Biogeography of Compositae 2nd Edition
Christoph Oberprieler, christoph.oberprieler@ur.de, Morgan Gostel, mgostel@fwbg.org

CAPITULUM and GCD
Mauricio Bonifacino, bonifacinoj@fagro.edu.uy,
Jennifer Mandel, jmandel@memphs.edu

CAPITULUM
THE INTERNATIONAL COMPOSITAE ALLIANCE NEWSLETTER

GUIDELINES FOR AUTHORS

Types of articles and editorial process

CAPITULUM accepts contributions matching the following sections, as long as they are relevant to the plant family Compositae (sunflower, daisy or aster family, a.k.a. Asteraceae). HEAD TOPICS & BREVIA: Section to showcase current research on Compositae. PIPET & PRESS: Articles about methods and techniques. THE HANDLENS: A close up look to a given species or morphological structure. THE CABINET: A window to the stories behind ancient or recent herbarium samples and the botanists behind them. FROM THE FIELD: The place where the bold and the adventurous share their latest finds in their eternal pursuit of the more recalcitrant comps. STYLE: Where science and art converge, artistic photography, botanical illustration or creative infographics. All is welcome if it comes with style. Manuscripts or photos intended for publication in CAPITULUM are to be submitted at www.compositae.org. Contributions will be sent to two external reviewers. Suggestions of suitable, qualified reviewers without conflicts of interest are encouraged.

General formatting and structure

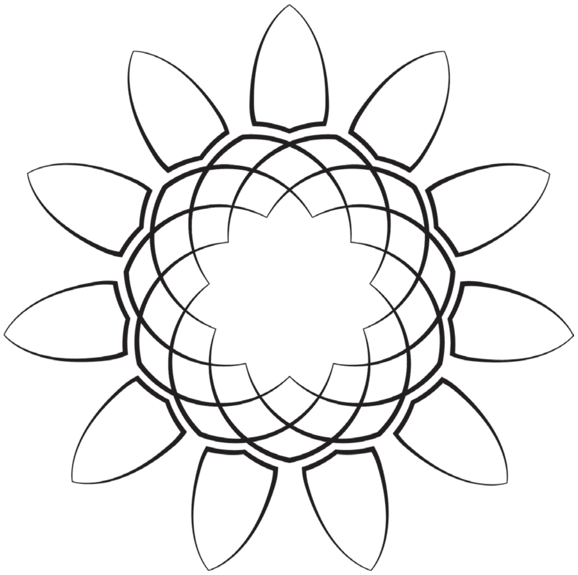
Consult a recent issue of CAPITULUM and follow these instructions. Language for submission is English. Use Times New Roman/Arial typography size 12. Provide a title and if needed, a subtitle. Include names of all authors, their ORCIDs, their professional affiliations and emails. Include a list of 5–6 keywords in alphabetical order. Provide an abstract of up to 250 words. There is no set structure on how to organize your text; however most cases will adapt well to the classic I-M&M-R-D plus Acknowledgements and Literature Cited;Tables; Appendices; and Figure Legends. Monographic works should include proper citation of names including types. Morphological descriptions, notes when needed, additional specimens examined (country, political division, political subdivision, locality, collector, collector #, date, herbarium code). Keys should be indented. Each couplet should be numbered 1a and 1b, 2a and 2b, etc. All scientific names at the rank of tribe or inferior should include authorship the first time they appear in the text, following Brummitt & Powell, Authors of Plant Names (Kew, 1992; info included in the International Plant Names Index [IPNI]). In text, a single space must follow a period, colon, semi-colon, or comma. Molecular phylogenetic and systematic studies should clearly state the sampling strategy including all details related to the sequencing and data analysis. Phylogenetic trees should have support values plotted.

Tables and figures

Tables must be prepared using MS Excel, please include different tables as different spreadsheets on the same file. Figures should be provided in either TIFF format (for photos) or as vector graphics such as AI or EPS for diagrams, illustrations, or phylogenetic trees. Maps should be provided as SHP files when possible or as vector graphics. You may send the photos and other graphics ordered and arranged following your preference, but you are advised that we could edit them to adjust them to CAPITULUM style. All figures must be uploaded as individual original files. Photos should be at least 300 dpi in resolution. Literature citation: please check that all your references are cited and vice versa. For the style of references check a recent issue of CAPITULUM.

Data availability requirements

CAPITULUM requires all data sets to be archived in a permanent, publicly accessible location. To enable readers to locate archived data, include a "Data Availability" section before the Literature Cited section. This should list the database, digital object identifiers (DOIs), stable URLs, and the respective accession numbers for all data from the manuscript, as appropriate. Note that accession numbers provided in a supplementary table (voucher table) accompanying the article do not need to be duplicated here in the data availability statement.



Magno amore in familiam Synantherearum captus
Lessing, 1829

TICA
THE INTERNATIONAL COMPOSITAE ALLIANCE